

# Contribution of Capture-Mark-Recapture Modeling to Studies of Evolution by Natural Selection

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**Abstract** Capture-Mark-Recapture (CMR) modeling is one of the most commonly used estimation methods in population ecology of wild animals. Until recently, much of the emphasis of this method was on the estimation of abundance and survival probability. Despite common interest in estimation of such demographic parameters, evolutionary ecologists have often been more critical of CMR estimation methods than wildlife biologists, mostly because the available models did not allow investigators to address what is at the heart of evolutionary ecology. Evolutionary ecology aims at explaining biological diversity: studies in this area of research necessarily involve assessment of variation in traits among individuals, including fitness components. The main limitation of early CMR models was the inability to handle *states* among which individuals move in a stochastic manner throughout life (e.g., breeding activity and number of offspring raised, locations, physiological states, etc.). Several important advances have enhanced ecologists' ability to address evolutionary hypotheses using CMR data; namely multistate models and models with individual covariates.

Recently, methodological advances have allowed investigators to handle random effects models. This is bringing CMR models close to modern statistical models (Generalized linear mixed models) whose use is rapidly increasing in quantitative genetics. In quantitative genetics, the *animal model* aims at disentangling sources of phenotypic variation to draw inferences about heritability of any type of trait (morphological, demographic, behavioral, physiological traits). The *animal model* partitions variation in the trait of interest using variance components. Understanding evolution by natural selection and predicting its pace and direction requires understanding of the genetic and environmental influences on a trait. Phenotypic characteristics such as morphological or life-history traits (i.e. demographic parameters such as number of offspring raised and survival probability) are likely to be influenced by a large number of genes, the genetic basis of which can be quantified via statistical inferences based on similarities among relatives in a population. The

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extent of evolutionary responses in a quantitative trait is assumed to be proportional to the force of natural selection and heritability of a trait. Estimating the genetic basis of quantitative traits can be tricky for wild animal populations in natural environments: environmental variation often obscures the underlying evolutionary patterns. However, this genetic basis of traits is at the heart of natural selection, and recently there has been increased interest in applying the *animal model* to natural populations to understand their evolutionary dynamics. Such models have been applied to estimation of heritability in life history traits, either in the rare study populations where detection probability is close to 1, or without considering the probability of detecting animals that are alive and present in the study area (recapture or resighting probability). Applications of the *animal model* to demographic parameters (fitness components) such as survival, breeding probability or to lifetime reproductive success in wild animal populations where detection probability is  $< 1$  require trans-disciplinary efforts; this is necessary to address evolutionary processes in such populations.

**Keywords** Capture-mark-recapture · Dispersal · Evolution · Fitness functions · Heritability · Life history theory

## 1 Introduction

Approaches to estimating demographic parameters using capture-mark-recapture data while accounting for incomplete detection of individuals by investigators during sampling sessions have tremendously diversified over the past 20 years (CMR estimation models; reviewed in Williams et al. 2002). Early efforts in development of CMR models have been directed mostly to estimation of abundance and survival probability, but recent advances now allow investigators to estimate other population vital rates such as breeding and recruitment probability, or movement probability among units of fragmented populations, temporary emigration, etc. (e.g., Spendelov et al. 1995, 2002; Pradel 1996; Pradel and Lebreton 1999; Oro and Pradel 2000; Schwarz and Arnason 2000, 2001; Schwarz and Stobo 2000; Nichols et al. 2000; Lindberg et al. 2001; Kendall and Bjorkland 2001; Lebreton et al. 2003; Reed et al. 2004; Barbraud and Weimerskirch 2005; Cam et al. 2005; Crespín et al. 2006; Hadley et al. 2006; Martin et al. 2006). In other words, CMR models allow estimation of the main parameters governing demographic processes. In addition, CMR models are now increasingly used to address community vital rates (e.g., species extinction or colonization probability; Nichols et al. 1998 a, b; Williams et al. 2002), and vital rates specific to large-scale features of species distribution (e.g., site occupancy models, MacKenzie et al. 2006). Recent technical advances relevant to the particular field of evolutionary ecology are extensively explained in Conroy (2008, this volume).

Recent CMR models aimed at estimating demographic parameters have two important features: (1) an increased variety of population vital rates can be estimated (provided appropriate sampling design), and (2) an increased degree of stratification

of populations can be achieved (i.e., classes in which individuals stay permanently or temporarily, or individual attributes) and stratum-specific vital rates can be estimated. This has partly alleviated an old tension between biologists and statisticians, the former blaming the latter for designing estimation methods corresponding to unrealistically simple populations or biological systems, the latter doubting that appropriate data could ever be collected to match the requirements of complex models (i.e., appropriate sampling design and large sample sizes in all strata within populations). Moreover, development of software programs and documentation has considerably facilitated access to CMR estimation techniques for biologists (some examples of software used in ecology, in alphabetical order: CAPTURE: White et al. 1978; Rexstad and Burnham 1991, MARK: White and Burnham 1999; Cooch and White 2007, MSURGE: Choquet et al. 2003, MSSURVIV: Hines 1994, POPAN: Arnason et al. 1998, SURGE: Clobert and Lebreton 1985; Lebreton and Clobert 1986, SURPH: Smith et al. 1994, SURVIV: White 1983). From the viewpoint of an evolutionary ecologist, an enormous stride has been made with the development of multistate models (e.g., Nichols and Kendall 1995). This was a first step towards accommodation of a pervasive property of the history of individuals in long-lived species: individuals change *state* (location, social or physiological state, etc.) in a stochastic manner.

CMR field techniques have long been popular among biologists (especially in studies of birds, small and large mammals, or fish). They have been widely used to estimate demographic parameters, but the corresponding statistical approaches disentangling sampling processes and demographic ones have not always been used (Martin et al. 1995). Not all the fields of ecology have taken full advantage of the potential that new CMR estimation models offer. The Proceedings of the 1994 EURING conference held at Patuxent Wildlife Research Center (Laurel, MD, U.S.A.) include a paper entitled: "Capture-recapture and evolutionary ecology: a difficult wedding?" (Clobert 1995; see also Clobert 2002). Despite the regular presence of researchers involved in evolutionary ecology studies at EURING meetings and the recent advances in CMR methodology applied to evolutionary studies, analytical tools that estimate demographic parameters of wild animal populations while accounting for imperfect detection of individuals do not seem as widely used in this field as in other fields of ecology, especially wildlife ecology and conservation biology. This probably partly results from differences in history and educational practices.

Although mathematics and statistics play an important part in education for evolutionary ecologists (e.g., Charlesworth 1994; Lynch and Walsh 1998; Caswell 2001), as far as estimation is concerned (e.g., genetic parameters; Lynch and Walsh 1998) analytical tools used typically do not account for the sampling processes that are specific to studies of wild animal populations, more precisely, incomplete detection of individuals (Martin et al. 1995). This may not be a problem for traits whose phenotypic values are independent of detection probability, but the assumption that the sample of captured or resighted individuals and the sample of undetected individuals have identical features is unlikely to be met for demographic parameters like breeding probability after recruitment (e.g., Nichols et al. 1994), age-specific

recruitment probability (e.g., Viallefont et al. 1995 a, b; Spindelov et al. 2002), breeding success probability or clutch size (e.g., Yoccoz et al. 2002).

Efforts to carefully design sampling protocols specific to wild animal populations and to master the corresponding statistical analyses (e.g., Williams et al. 2002) are probably more common in education programs offered to students in wildlife ecology and conservation biology than to evolutionary ecologists. There is no international review available on the topic, but when one scans web sites detailing course sequences offered in undergraduate and graduate programs organized by evolutionary ecology departments, classes on CMR modeling hardly ever appear. Such classes appear in several wildlife ecology programs offered in internationally known universities. Because it is necessary to have accurate estimates of demographic parameters to assess the state of populations, design efficient management plans and make decisions, not accounting for sampling “biases” that have long been known (e.g., Cormack 1964; Jolly 1965, 1993; Seber 1965; Lebreton et al. 1992) may be considered more “irresponsible” in wildlife ecology educational programs (Anderson et al. 2003) than in others. The quantitative content of university programs for wildlife ecology may be considered as insufficient by quantitative wildlife ecologists, but there is some pressure in specialized scientific journals to develop quantitative skills in education (e.g., Kendall and Gould 2002; Seber and Schwarz 2002; Anderson et al. 2003).

Because wildlife ecologists focus on wild animal populations, they are constantly faced with the challenge of using or designing appropriate approaches for analysis. This is not true for evolutionary ecologists. The discipline differs from that of wildlife ecology in that there are strong historic relationships with some other disciplines that tend to utilize experimental study systems and molecular approaches to address the genetic basis of evolution (e.g., evolutionary biology, molecular evolution, phylogeography, population, quantitative and developmental genetics, systematics, etc.; e.g., Freeman and Herron 2000). Students in evolutionary ecology devote a large proportion of time to these fields and may not be introduced to the specificity of the data and analytical tools required to conduct demographic studies in wild animal populations (e.g., non-detection of marked individuals that are alive and present in the study area). Nevertheless, comparative methods play an important part in evolutionary ecology (e.g., life history evolution and evolution of morphological traits; Promislow et al. 1992; Bennett and Owens 2002; Liker and Székely 2005) and such studies are unlikely to be possible without using data from wild animal populations, especially for long-lived species. Several comparative studies have ignored the distinction between studies that have estimated demographic parameters while accounting for incomplete detection of individuals, and those that have not, even in situations where survival probability was the focal trait (e.g., Owens and Bennett 1994; Liker and Székely 2005). Use of estimates of demographic parameters ignoring incomplete detection of individuals may lead to erroneous conclusions.

Almost 15 years later, the answer to the question: “Capture–recapture and evolutionary ecology: a difficult wedding?” (Clobert 1995) may not be unanimous in the EURING meeting audience. Despite the slowness of integration of CMR estimation models in evolutionary ecology, the range of questions relevant to evolutionary ecology addressed in studies that have used appropriate CMR estimation techniques

is large. In addition, recent advances in development of CMR models may open new opportunities for evolutionary ecologists to use empirical data from wild animal populations to address novel questions. In the following Section (2), I will address the specificity of evolutionary ecology as a discipline. If evolutionary ecology has generally been viewed as relevant to basic research exclusively, several researchers are now advocating consideration of the theoretical framework of (micro-) evolution to address questions about ecological processes and the consequences of human influence on wild animal populations and their habitat (e.g., Ferrière et al. 2004; Reznick et al. 2004). In Section 3, I will define natural selection, one of the corner stones of evolutionary ecology. In this section, I will also describe how the specific question of the evolution of demographic parameters is usually addressed. Understanding how natural selection is addressed in wild animal populations is necessary to assess the features of existing CMR studies in evolutionary ecology, which I will do in Section 4. Concerning the evolution of demographic parameters by natural selection, up to now CMR estimation techniques have been used to address only part of the prerequisites for natural selection. A central prerequisite, heritability, has not been addressed. Recent advances in estimation methods used in quantitative genetics and in methods aiming at estimating demographic parameters from CMR data have some common features that should be useful to address heritability. In Section 5, I will describe the method used in quantitative genetics with data from wild animal populations to address heritability of traits (the *animal model*), and I will offer suggestions concerning the type of development needed in CMR estimation models to address heritability in demographic traits.

## 2 Evolutionary Ecology: Historical Background

There have been numerous attempts to classify the different disciplines of biology “to deal with the enormous range of phenomena brought together under the heading of biology” (Mayr 1997, p. 111). According to Mayr (1997), classification of disciplines according to the type of question asked in research is one of the most logical classification systems. There are three main questions: “What?”, “How?”, and “Why?” However, the first question, “What?”, is shared by all biological disciplines. Description (establishment of a “solid factual basis”) is the first step in any branch of biology. However, “Answers to the ‘What?’ questions alone failed to produce a satisfactory solution to the problem of how to classify the subdivisions of biology” (Mayr 1997, p. 115). In addition, it is impossible to conduct any descriptive work without identifying the object to describe. Identification of the objects on which scientific research focuses in different biological disciplines is possible because there are specific theoretical bodies. Description cannot be conducted without referring to a theoretical background because no “factual basis” emerges *ex nihilo*, independently of the hypotheses and theories. Consequently, answers to the “What?” question depend on identification of biological disciplines using other criteria.

Answers to the “How?”, and “Why?” questions provide a more efficient basis for classification of biological disciplines – a distinction that appeared in 1870 in

debates among biologists. Biology has considerably diversified since then, but a fundamental distinction between disciplines has survived, even if this classification system has its problems. The main distinction between these two types of questions lies in the type of causes invoked to explain biological phenomena. Proximate causes allow investigators to explain the functioning of biological entities “here” and “now” (answers to the “How?” question). Conversely, ultimate causes allow investigators to explain observed phenomena in the light of the history of life and evolutionary theory (answers to the “Why?” question). “Why?” questions usually relate to adaptation or organic diversity (Mayr 1997, p. 118); “ultimate causes attempt to explain why an organism is the way it is, as a product of evolution”. [. . .]. However, “no biological phenomenon is fully explained until both proximate and ultimate causes are illuminated”. “One of the special properties of the living world is that it has these two sets of causations.” (p. 67).

Mayr (1997) also described ecology as the most heterogeneous and comprehensive field of biology, and one that is difficult to assign to one single type of question (“How?”, or “Why?”): both types of questions are addressed. Ecologists focusing on ultimate causes are called *evolutionary ecologists* (Fox et al. 2001). According to Fox et al. (2001), “Evolutionary ecology and ecology share the goals of describing variation in natural systems and discovering its functional basis. Within this common framework, evolutionary biologists emphasize historical and lineage-dependent processes and hence often incorporate phylogenetic reconstructions and genetic models in their analyses. Ecologists, while cognizant of historical processes, tend to explain variation in terms of contemporary effects of biotic and abiotic environmental factors. Evolutionary ecology spans the two disciplines and incorporates the full range of techniques and approaches from both”

The apparent difference between the timescales invoked in ecology and evolutionary ecology may lead to the conclusion that the dichotomy is natural. However, this traditional dichotomy may have become an obstacle to our understanding of ecological phenomena, and this may have consequences on our ability to design efficient conservation plans. There is growing evidence that evolutionary responses to environmental changes can be so fast that researchers are able to witness them both in the laboratory and in the wild (Ferrière et al. 2004; Frankham and Kingsolver 2004; Reznick et al. 2004). Hendry and Kinnison (1999) suggested that rapid microevolution is the norm in contemporary populations confronted with environmental change. According to Saccheri and Hanski (2006), “there is a growing acceptance that the traditional dichotomy between ecological and evolutionary timescales is a false one”.

## **3 Evolution by Natural Selection**

### ***3.1 Natural Selection***

“Evolution may be defined as any net directional change or any cumulative change in the characteristics of organisms or populations over many generations [. . .]” and

“may occur as a result of natural selection, genetic drift, or both” (Endler 1986, p. 5). According to Fairbairn and Reeve (2001, p. 30),

Natural selection is notoriously difficult to define. In the broadest sense, the process of natural selection has been defined by the following deductive argument:

If there is:

- (i) variation in some attribute or trait among biological entities (phenotypic variation),
- (ii) a consistent relationship between the trait and fitness (a fitness function), and
- (iii) descent with heritability for the trait (i.e., the variation in the trait must have a genetic component),

Then the trait distribution will change:

- (I) within generations more than expected from ontogeny alone, and
- (II) across generations “in a predictable way” until an equilibrium is reached.

This definition is true to Darwin’s original description of natural selection, and was adopted by Endler (1986) in his review of selection in natural populations. However, in addition to being rather cumbersome, the deductive argument is flawed because conclusion (I) does not require premise (iii) and holds for any fitness difference caused by differences in survival (i.e., differences in fecundity alone will not cause within-generation changes in trait distributions) In constructing a more concise and logically consistent definition of natural selection, most authors (e.g., Lande and Arnold 1983; Futuyma 1998) prefer to distinguish the process of natural selection occurring within generations (premise i and ii) from the evolutionary consequences of that selection (premise iii and conclusion II)

Researchers working in different areas have used different definitions of fitness (Endler 1986, p. 38). In life history theory, the fitness concept currently relies on invasibility: the possibility of a rare mutant strategy to replace the strategy played predominantly in the population (Metz et al. 1992). However, as emphasized by Brommer et al. (2002), invasibility is not readily measured in natural populations, and many empirical studies focus on other measures of evolutionary success. When focusing on selection at the level of individual organisms, fitness “in its most general sense is success in contributing descendants to the next generation” (Fairbairn and Reeve 2001, p. 31). The definition of fitness by Endler (1986, p. 39) highlights the direct relevance of CMR estimation models to evolutionary ecology: “Fitness is the degree of demographic difference among phenotypes”, or a measure of the degree of the following condition for natural selection: “a consistent relationship between [a] trait and mating ability, fertilizing ability, fertility, fecundity, and or survivorship”. Natural selection is based on demographic processes, and estimation of demographic parameters is a key point in some approaches to detecting natural selection (Endler 1986).

### ***3.2 Evolution of Demographic Parameters by Natural Selection***

Demographic parameters (i.e., age at maturity, number of offspring produced, longevity, age-specific reproductive investment and mortality schedule, etc.) are not only involved in the evolution of morphological, behavioral, or physiological traits by natural selection, but they are themselves subjected to natural selection (Roff

1992; Stearns 1992). The field of life history evolution focuses on the evolution of demographic parameters, a class of traits also called *fitness components* (Stearns 1992)

Studies of the evolution of demographic parameters do not necessarily address all the above Premises: some studies do not require Premise (ii) because they do not involve other classes of traits than fitness components themselves. Such studies involve two fitness components (or more), and Premise (i) concerns several components simultaneously. In life history theory, it is assumed that there are relationships among traits and that natural selection operates on complexes of traits: “Age-specific survival and fecundity are not free to independently evolve, but are constrained by physiological and ecological trade-offs” (Tatar 2001). As emphasized by Clobert (1995), Viallefont et al. (1995a) and Cooch et al. (2002), reproductive costs and trade-offs between life history traits are central to the theory of life history evolution (Reznick et al. 2000). The basis of physiological trade-offs (Stearns 1992) is the following: because individuals have access to limited resources, resources allocated to one trait are assumed not to be allocated to another (*Principle of allocation*, Levins 1968). According to Reznick et al. (2000), “[...] it became convenient to think of the life history as being similar to a pie divided into slices, each slice being devoted to a different function, such as growth, maintenance, storage or reproduction. Because the pie is of fixed size, increasing the size of a given slice necessarily decreases the size of another slice”. For example, individuals that raised two offspring to independence in a given breeding occasion may not be able to invest the same amount of energy in their own maintenance functions as individuals that raised only one offspring, and the former may incur survival costs. Trade-offs may also have a behavioral basis when reproductive activity is associated with increased mortality risk because of predators or fights with conspecifics. Last, there are inter-generational trade-offs linking parental allocation of resources to reproduction and offspring fitness (e.g., offspring size at birth; Stearns 1992).

Trade-offs also play a central part in one of the evolutionary theories of senescence: antagonistic pleiotropy (Williams et al. 2006). Antagonistic pleiotropy assumes that “improvements early in life are purchased at a cost to later-age fitness components” (Williams et al. 2006). Several hypotheses have been put forward concerning the mechanisms responsible for pleiotropy (Tatar 2001), but one of them is based on physiological trade-offs: “For instance, the allocation of lipid to current egg production may preclude its use in cell or mitochondria cell membrane turnover. Natural selection favors genotypes that maximize fitness within such sets of constraints” (Tatar 2001, p. 131). Studies of antagonistic pleiotropy may address covariation between age at maturity and at last reproduction. Here, Premise (ii) isn’t relevant.

However, traits other than fitness components may be taken into account in studies of life history evolution, even if the evolution of such traits isn’t the central topic of these studies. For instance, variation in fitness components such as fecundity (e.g., number of eggs in fish) may be intrinsically linked to variation in morphological traits such as body size (*n.b.*: here *fecundity* describes the actual reproductive performance; see Caswell 2001, p. 10, for an alternative definition from human

demography). Consequently, studies of the evolution of demographic parameters by natural selection may address Premise (ii): a consistent relationship between a (non-demographic) trait (e.g., morphology) and fitness. However, in studies of life history evolution involving morphological traits, the latter are usually addressed as part of a trio including two fitness components. In the above example (fecundity and body size), in species with delayed maturity, changes in age at maturity may result in changes in body size, which in turn may result in changes in fecundity (Roff 2001). In other words, body size is involved in the trade-off between development time (age at maturity) and fecundity.

#### 4 Features of Existing CMR Studies in Evolutionary Ecology

CMR estimation models have been used in evolutionary ecology studies addressing evolution of “non-demographic traits”. For that class of traits (i.e., morphological, physiological, behavioral traits) CMR estimation methods have been used to address Premise (ii), i.e., to estimate fitness components and assess fitness functions (e.g., Gimenez et al. 2006). Apart from estimation of fitness components, CMR estimation models may be considered to address other Premises for natural selection and Deductions I and II. For morphological, behavioral or physiological traits, the question of whether samples are representative in studies addressing Premises (i) and (iii) in the above definition of natural selection, or Deductions I and II, should probably receive attention. If detected and undetected individuals have different characteristics with respect to the trait of interest (e.g., if there is a relationship between size or color and detection probability), then use of CMR estimation models may be necessary to assess the distribution of trait values in populations (in this case closed-population models may be useful to estimate the frequency of trait values). In most studies, the observed distribution of phenotypic trait values in samples is assumed to reflect the distribution of trait values in populations in an exhaustive and consistent manner (i.e., samples are assumed to be representative of (sub-) populations). In addition, multitrait *animal models* (see Section “Multitrait Models”) or random coefficients *animal models* (Schaeffer 2004) can be used to address fitness functions based on breeding values (a possible approach to Premise (ii)) and heritability (Premise (iii)) of traits changing over life (e.g., body size in some mammal or snake species, egg size in some bird species). In this case, repeated data from individuals are needed. For continuous traits, this may raise the issue of missing individual covariates when individuals are not recaptured or resighted (Bonner and Schwarz 2004), an area where methodological development is needed. In most studies, data are assumed to be missing at random (e.g., missing data in growth curves).

Concerning the evolution of demographic parameters themselves, Premise (i) (phenotypic variation and covariation between parameters) has been addressed using CMR estimation models, as well as Premise (ii) when morphological or physiological traits are assumed to be involved in the trade-offs between demographic parameters. I am not aware of studies that have addressed Premise (iii) using CMR

estimation models (Premise (iii) is the third condition for evolution of demographic parameters by natural selection: heritability). Interestingly, CMR estimation models required to address Deduction I (within-generation selection) have been developed (Burnham and Rexstad 1993; Pledger and Schwarz 2002; Royle and Link 2002; Royle 2007), but I am not aware of studies that have addressed the evolutionary consequences of selection (Deduction II) for demographic parameters using CMR estimation techniques.

Despite the relatively “limited” scope of the evolutionary ecology studies that have used appropriate CMR estimation models (several aspects of natural selection have not been addressed), such studies have required considerable efforts from biologists and statisticians: details of the technical advances are reviewed in Conroy (2008, this volume). In this section, I will focus on some evolutionary ecology studies that have accounted for incomplete detection of animals to estimate demographic parameters. This is not an exhaustive review; my goal is to provide examples illustrating the diversity of topics addressed.

## ***4.1 Life History Evolution***

### **4.1.1 Trade-offs Between Life History Traits**

Trade-offs are one of the topics that have been addressed in the largest proportion of CMR studies in evolutionary ecology (e.g., Nichols et al. 1994; Nichols and Kendall 1995; Viallefont et al. 1995a, b; Cam et al. 1998; Yoccoz et al. 2002; Barbraud and Weimerskirch 2005). In a large number of cases, the studied species exhibited a small range of reproductive investment levels (e.g., non-breeding versus a single egg produced in birds or a single young in mammals, or only two or three young raised; McElligott et al. 2002; Barbraud and Weimerskirch 2005). In such long-term observational studies that have retrospectively used data collected over long periods of time, trade-offs have been addressed using few discrete categories of reproductive investment, as opposed to continuous trade-off functions (Reekie et al. 2002). Technical development in CMR estimation methodology in the 1990’s has considerably broadened the scope of studies aimed at detecting trade-offs. First, in iteroparous species, the proportion of individuals breeding more than once is larger than 0, which implies that individuals may change breeding *state* (i.e., breeding activity or success; Nichols et al. 1994) over time and raise a different number of offspring to independence on different breeding occasions. For this reason, development of multistate models has played a central part in studies of trade-offs (Arnason 1973; Brownie et al. 1993; Nichols and Kendall 1995; Williams et al. 2002; Conroy 2008 this volume). Several versions of multistate models have been designed to estimate state-specific transition probabilities in situations where there are unobservable states or where individuals are sometimes misclassified (e.g., when individuals are erroneously considered as nonbreeders in a given sampling occasion; Kendall and Nichols 2002; Kendall et al. 2003; Kendall 2004; Nichols et al. 2004). These tools allow investigators to accommodate situations that are common in empirical

studies (i.e., state uncertainty). In addition, development of models allowing use of different sources of data provides a means of improving estimates of local survival probability by estimating permanent emigration (Burnham 1993). Indeed, unless an additional source of data is available, estimates of local survival incorporate permanent emigration out of the study area. The ability to disentangle the factors influencing “true” local survival and those influencing dispersal is important for studies of trade-offs between survival and other life history traits. Unfortunately, studies in evolutionary ecology mostly use live captures/resightings of marked animals, partly because study systems focusing on hunted species may be considered as “artificial”. However, there may be situations where selective hunting may correspond to carefully designed experimental systems that have played a major role in development of theory in evolutionary ecology (e.g., Mertz 1975).

Before multistate models became standard, other approaches were possible (reviewed in Viallefont et al. 1995a); for example one may compare survival probability in individuals assumed to have identical reproductive history (e.g., first time breeders with no prior experience). That is, groups of individuals are defined on the basis of the number of offspring raised in the first breeding occasion, and group-specific survival probabilities over the first year of reproductive life are compared. Alternatively, experiments may be conducted by randomly assigning “identical” individuals (i.e., same age, same year, same environmental condition, same prior reproductive history etc.) to treatments (increased/decreased clutch or brood size). The underlying assumptions are that no important factor influencing survival probability has been missed (left uncontrolled), and that the controlled factors correctly reflect the factors involved *in natura* in the studied process (the factors have been correctly identified). In some instances, recapture probability in the year following the first breeding attempt has been compared to subsequent recapture probability to address possible experience-related reproductive costs in terms of future reproduction, assuming that recapture probability reflects breeding probability to some extent (Viallefont et al. 1995b). Last, temporary emigration has also been used as an indicator of breeding probability (e.g., Kendall and Nichols 1995; Schmidt et al. 2002; Frétey et al. 2004).

Progressively, more complex definitions of state have been used to address the question of trade-offs more thoroughly. More complex multistate models incorporating individual covariates have also been developed. Indeed, because individuals vary in their ability to obtain resources, or because they live in environments with different resource availability (Stearns 1992), reproductive costs may not be identical in every individual; i.e., some individuals may be able to invest more in reproduction without incurring as large costs as others, depending on their state. Here, state may correspond to different things depending on the organism studied (e.g., body size, parasite load, immunological state, social dominance, experience, etc.). State is assumed to reflect a hierarchy among individuals in their ability to acquire resources or to use them, or simply a baseline efficiency of functions (e.g., maintenance, reproduction, etc.). Detection of reproductive costs from observational data requires comparison of fitness between individuals having different condition or social rank but identical reproductive investment (reproductive activity and success).

Using states combining information from reproduction and other individual characteristics (e.g., experience), multistate models allow investigators to address trade-offs in heterogeneous populations. Development of models including individual covariates (e.g., body mass or size; Bonner and Schwarz 2004) has played a large part in emergence of studies addressing state-specific reproductive costs and reproductive tactics (e.g., Barbraud and Weimerskirch 2005).

Moreover, temporal environmental variation (i.e., variation in resource availability or density of conspecifics) may lead to time-specific variation in reproductive costs within categories of individuals in the same state in different years (Orzack and Tuljapurkar 2001). Assuming that individuals are able to assess resource availability in time, individuals may adjust the amount of energy allocated to functions according to their state; i.e., there may be *individual optimization* (Van-Noordwijk and de Jong 1986; Pettifor et al. 1988, 2001; Tinbergen and Both 1999). If individual optimization occurs, only experimental approaches (e.g., Yoccoz et al. 2002) may allow detection of trade-offs. The difficulty in designing appropriate experiments to address trade-offs has been discussed in Cooch et al. (2002, p. 35): “Trade-offs within an individual must be true (Tuomi et al. 1983; Emlen 1984); if an individual is forced to expend greater energy on one activity, then this necessarily reduces the amount of energy available for another activity. However, this does not necessarily mean that trade-offs occur among individuals. This is important, since natural selection operates on the additive genetic covariance among individuals, not correlations within individuals”. If trade-offs are necessarily based on physiological or behavioral mechanisms operating at the individual level (trade-offs “within” individuals), addressing relationships between fitness components by comparing different individuals assigned to different experimental treatments (or naturally exhibiting different levels of reproductive investment) is addressing relationships between components expressed “among” individuals (trade-offs “among” individuals). Comparing different individuals should allow inferences about within-individual trade-offs if investigators can be sure that individuals are strictly identical with respect to all traits except the ones involved in the trade-off itself, but failure to fulfill this condition is thought to be a major reason for failure to detect trade-offs.

The process of individual optimization is assumed to lead individuals to make decisions according to their current state. State may change over time, but there may also be permanent differences among individuals. CMR studies have contributed to identification of permanent differences among individuals. For example, several studies have provided evidence of permanent differences in fitness components (e.g., survival probability) among individuals according to morphological traits reflecting relative body conditions (e.g., Barbraud and Weimerskirch 2005; Blums et al. 2005). Similarly, long-lasting cohort effects have been identified (e.g., Cam et al. 2005), as well as a permanent influence of conditions during development on several life history traits (e.g., Cam et al. 2003). Blums et al. (2005) have used relative time of nesting to account for individual differences in “quality”. Experimental studies have provided contrasting results concerning the hypothesis of individual optimization in wild animal populations (e.g., Tinbergen and Sanz 2002; Török et al. 2004). However, in all cases tests of this hypothesis require high levels of stratification of

the data according to state (which may be assigned to individuals in the framework of an experiment) and year or environmental conditions (biotic and abiotic).

Last, some of the physiological and behavioral mechanisms underlying intra- and inter-generational trade-offs between life history traits have been investigated using CMR estimation models. For instance, in an experimental study, Reed et al. (2006) have addressed the relationship between survival probability and manipulated testosterone level in free-living dark-eyed juncos (*Junco hyemalis carolinensis*). Testosterone-treated males increased levels of activity and home range size and had elevated levels of stress hormones. They exhibited increased ability to attract females (increased ability to produce extra-pair offspring), but produced smaller offspring with lower postfledging survival. In addition testosterone-treated adult males had increased detectability and susceptibility to predation, which led to lower adult survival.

#### **4.1.2 Level at Which Natural Selection Operates and Estimation of Demographic Parameters**

Obviously, modern CMR estimation models allow evolutionary ecologists to address a large range of questions directly relevant to fitness functions, selection, and adaptation. However, the ultimate goal of evolutionary ecologists is to address differences in demographic parameters at the level at which natural selection operates, which is often identified as the individual level (Endler 1986). Mayr (1997) identified a reason why evolutionary ecologists constantly press statisticians to develop complex CMR models allowing investigators to stratify populations according to large numbers of criteria (e.g., multistate models, models with time-varying individual covariates; Pollock 2002). This is an irresolute tension between the conceptual foundations of evolutionary ecology and population ecology which was extensively discussed in Cooch et al. (2002). The community of researchers involved in development and use of CMR estimation models is mostly composed of researchers focusing on wildlife ecology and conservation biology, or of statisticians who often develop models to answer questions from these same fields of ecology. Historically, these fields have been dominated by concepts from population ecology, which “can be tracked back to a school of mathematical demographers interested in the growth of populations and the factors controlling it” (Mayr 1997, p. 211). However, the population concept specific to population ecology is different from that of evolutionary ecology. “The population concept adopted by most mathematical population ecologists was basically typological, in that it neglected the genetic variation among the individuals of a population. Their ‘populations’ were not populations in any genetic or evolutionary sense but were what mathematicians refer to as sets. The crucial aspect of the population concept to have emerged in evolutionary biology, by contrast, is the genetic uniqueness of the composing individuals. This kind of ‘population thinking’ is in sharp contrast with the typological thinking of essentialism. In ecology, the genetic uniqueness of the individuals of a population is usually ignored” (Mayr 1997, p. 211).

Ideally, evolutionary ecologists would like to apply this concept of genetic “uniqueness” of individuals to demographic parameters as well. This is because “the ultimate context for estimation is the degree to which selection and the fitness differences upon which selection operates translates into evolutionary change” (Cooch et al. 2002). Indeed, the individual level is assumed to be the relevant level of selection in many studies (Endler 1986). However, as Nichols (2002, pp. 49–50) pointed out, “[...] the larger the number of strata, the fewer individuals in each stratum, and the more difficult it will be to estimate stratum-specific survival probability. [...] increasing stratification will yield a single individual in each stratum, with the corresponding estimation problem analogous to that of being asked to estimate the probability of heads from a single flip of a loaded coin. [...] some form of aggregation is necessary for the conduct of science. [...] If we view an individual organism’s fate or behaviour at any point in space and time as a unique event not capable of informing us about the likelihood of the event for other individuals or points in space and time, then generalization and prediction become impossible. The task of the biologist then involves simply recording and describing these unique events and possibly developing a posteriori stories to explain them. Although such descriptive work might be interesting, it is not consistent with most definitions of science”.

Stratification in large numbers of discrete categories and limited sample size makes statistical inference impossible. However, evolutionary ecologists are familiar with an approach assuming that phenotypic traits of individuals in a population are characterized by a distribution. The distribution is assessed using random individual effects models, also called *frailty* models in human demography (Vaupel and Yashin 1985a, b; Service et al. 2000; Cam et al. 2002a; Link et al. 2002a, b; Service 2004; Wintrebert et al. 2004; Fox et al. 2006). Mixed models (Fahrmeir and Tutz 1994) are extensively used in quantitative genetics to address the genetic basis of phenotypic values of quantitative traits in populations (i.e., as opposed to “qualitative traits” such as gender); more precisely to assess their variance in populations (Lynch and Walsh 1998). Mixed models are commonly used in human demography to address senescence (e.g., Yashin et al. 2001; Service 2000, 2004), and they are also used in studies of behavior (e.g., Hernández-Lloreda et al. 2003). The motivations for the use of mixed models in these different fields have common points: (i) incorporation in statistical models of terms accounting for heterogeneity among individuals in the focal trait, (ii) the possibility for dependence of individuals for trait values (e.g., incorporation of a particular variance–covariance matrix for random effects), and (iii) assessment of the influence of specific covariates (fixed effects) on the trait while accounting for specific variance–covariance structures for random effects.

### The Process of Natural Selection: Within-Generation Mortality Selection

Several long term studies have provided evidence that wild animal populations are demographically heterogeneous (e.g., Fox et al. 2006): it has been suggested that populations are composed of groups of individuals with a permanent hierarchy in fitness components among individuals. Whenever measurable individual

characteristics can be used to account for individual heterogeneity in a satisfactory manner, individual covariates may be used (e.g., Blums et al. 2005). However, studies of survival in humans have provided evidence that measurable covariates are not always sufficient to account for heterogeneity among individuals (Hougaard 1991). In this case the hierarchy among individuals can be accounted for in discrete time survival models by incorporating an individual random effect with mean 0 and a variance term accounting for the distribution of individual survival probability around the mean (Cam et al. 2002a, Link et al. 2002a, b). The mean survival probability may depend on fixed effects such as age, sex, year, birth cohort, etc. These models assume that there are differences in *underlying*, or *latent* survival among individuals (Cooch et al. 2002). The same approach can be used to model underlying differences in breeding probability or breeding success probability among individuals.

Under the *good genes hypothesis*, some individuals are assumed to have a higher breeding success probability than others, or higher survival probability, or both (e.g., Curio 1983; Cam et al. 2002a; Link et al. 2002a, b). This is likely to have consequences for studies of senescence or any class of age effect on demographic parameters (Curio 1983; Vaupel and Yashin 1985a, b). In heterogeneous populations, one might expect an age-related change in the composition of the population. The *selection hypothesis* accounts for the progressive concentration of individuals with higher intrinsic survival probability in older age classes (Endler 1986), and if there is a positive correlation between breeding success probability and survival at the individual level, the progressive concentration of individuals with higher success probability in older age classes (Cam et al. 2002a; Barbraud and Weimerskirch 2005; Beauplet et al. 2006). This within-generation phenotypic selection process corresponds to Deduction I in the definition of natural selection (see Section 3.1). Within-generation phenotypic selection is not a sufficient condition for natural selection, but this process may explain some within-generation changes in survival or reproductive parameters detectable in heterogeneous populations (e.g., Forslund and Pärt 1995; Service 2004). More generally, assessment of phenotypic variation in fitness components among individuals within populations (e.g., Fox et al. 2006) is at the heart of studies of life history evolution by natural selection and is relevant to studies of the evolution of traits other than age-specific life histories (Mazer and Damuth 2001).

Senescence has been detected in a fair number of wild animal populations using CMR estimation models (e.g., Nichols et al. 1997; Festa-Bianchet et al. 1999; Bryant and Reznick 2004; Gaillard et al. 2004), and is common in captive birds and mammals (Ricklefs 2000; Ricklefs and Scheuerlin 2001). Senescence has motivated an enormous number of studies in humans, probably because of the economical and sociological implications of the phenomenon. In addition, senescence is one of the most challenging paradoxes from a fundamental perspective: “Senescence is an intriguing problem for evolutionary theory: can natural selection favour an age-specific decline in fitness?” (Bennett and Owens 2002). Not all authors agree on the occurrence of senescence in wild vertebrates. According to Williams (1992) “Both birds and mammals have life cycles that should make them similarly

vulnerable to the evolution of senescence, but there is little evidence that senescence affects birds at all. Where data on avian age structures are most abundant, it usually appears that mortality rates of young adults prevails through life. This conspicuously violates expectation from theory” [of Hamilton 1966]. However, as emphasized by van de Pol and Verhulst (2006); “Phenotypic traits can change as a result of within-individual changes (phenotypic plasticity) and between-individual changes, as selection may favour some individuals over others. When quantifying how population values of phenotypic traits change over time or differ between groups of individuals, it is therefore important to realize that both within–and between–individual process might be underlying causal mechanisms”. Individual heterogeneity may mask senescence and patterns of change in life history traits over life, or may hamper quantification of the rate of change in fitness components with age (Service 2004; van de Pol and Verhulst 2006).

### Development of *frailty* CMR models

Until now, estimating individual variation in life history traits without using observable covariates, and estimating age-specific variation in life history traits (e.g., survival probability) while accounting for individual heterogeneity in underlying survival probability were difficult because methods were not designed to handle incomplete detection of individuals. The very first CMR estimation models developed to address heterogeneity in survival probability were developed in the 1970s. The development of models accounting for individual heterogeneity in parameters was motivated by the issue of heterogeneity in detection probability among individuals. The importance of such heterogeneity in wild animal populations has long been acknowledged (e.g., Carothers 1973; Gilbert 1973; Pollock et al. 1990; Norris and Pollock 1996; Pledger and Efford 1998; Pollock 2002; Link 2004): for example, failure to account for such heterogeneity may result in biased estimates of survival probability in open population models or of population size in both closed and open populations models. Efforts to account for heterogeneity in detection probability have triggered development of models accounting for individual heterogeneity in other parameters (e.g., survival; Burnham and Rexstad 1993; Pradel et al. 1995; Burnham and White 2002; Pledger and Schwarz 2002; Royle 2007).

Recently developed CMR estimation models allow consideration of heterogeneity in survival via random individual effects (Royle 2007). The state-space formulation of the Cormack–Jolly–Seber model proposed by Royle (2007) offers flexible means of extending the model to account for the specificity of different study systems and sampling schemes, and address different biological hypotheses. Briefly, the model accounts for the individual *state* on a given sampling occasion (e.g., dead or alive), and is specified using two distinct models: one for the process of interest (i.e., the survival process over a given time interval, partly unobservable), and one for the observations (i.e., whether the individual was captured/resighted on a given occasion). The observation process depends on recapture/resighting probability, and is conditional on the *latent* survival process (i.e., survival probability). Survival probability can be modelled as a function of covariates such as year, age,

environmental covariates, individual measurable characteristics (e.g., body size etc.), and an individual random effect if one has reasons to suspect additional heterogeneity in survival probability (e.g. Royle 2007). With this innovation, frailty (Yashin et al. 2001) CMR models can be developed. Parameters in this class of models can be estimated using a Bayesian approach (e.g., using WinBUGS; Spiegelhalter et al. 1996). In addition, it is theoretically possible to design a state-space formulation of the multistate Arnason-Schwarz model (Arnason 1973; Dupuis 1995) with frailty, by using an additional (partially unobservable) transition process conditional on survival (i.e., a process accounting for the probability of being in a given stratum in a given occasion, and transition probability among strata in consecutive sampling occasions).

### 4.1.3 Individual Fitness and Population Growth Rate

On a related topic, Link et al. (2002a) used correlated latent survival, breeding and probability of raising 1 or 2 offspring to independence to estimate individual fitness. As emphasized above, estimation of fitness is at the heart of studies of evolutionary change by natural selection. Many empirical studies of selection have used fitness components to address fitness functions, but there is increased interest in developing estimates of “total fitness” (not components only; e.g. Coulson et al. 2006). Ideally, one may want to estimate an “individual growth rate” measuring the capacity of a given phenotype to be propagated into future generations. Because the growth rate of a genotype depends on the timing of production of viable offspring during life (Brommer et al. 2002), McGraw and Caswell (1996) suggested using an individual-specific Leslie matrix to estimate fitness. Link et al. (2002b) assessed the performance of the growth rate estimated using individual-specific Leslie matrices as an estimator of individual fitness. They defined latent fitness as the “latent individual growth rate”, which corresponds to the latent survival characterizing the individual, as well as the individual breeding probability, and probability of producing a given number of offspring. They concluded that individual capture–recapture history data (i.e., one realization of the stochastic process defined by latent life history traits, McGraw and Caswell 1996) result in realized fitness that isn’t consistent with latent fitness, and advocated a model-based approach to estimating fitness.

Interestingly, the distribution of individual demographic parameters (i.e., latent parameters) in populations has received much attention in another field, namely, applied population dynamics and conservation biology. Indeed, Conner and White (1999), Kendall and Fox (2001, 2003), and Fox and Kendall (2002) have provided evidence that certain forms of demographic heterogeneity substantially influence population persistence, a question that is particularly relevant to small populations. Development of CMR estimation models allowing investigators to estimate the distribution of individual life history traits and the possible covariation among latent traits may help develop an empirical basis for investigations of population persistence.

## 4.2 Evolution of Morphological and Behavioral Traits

CMR studies have also contributed to investigations of covariation between morphological or behavioral traits and fitness components. Just like for life history evolution, most CMR studies have addressed fitness functions and have drawn inferences about the possible consequences of these functions in terms of natural selection. However, I am not aware of studies that have addressed fitness functions of physiological traits using CMR estimation models, apart from the study by Reed et al. (2006, see above) whose aim was to investigate the physiological mechanisms underlying trade-offs between life history traits in juncos. The fitness costs incurred by testosterone-treated males suggest that high-testosterone phenotypes have selective disadvantages *in natura*. The body of studies listed below may seem eclectic compared to studies of life history evolution for two reasons. First, whether a trait is under selective pressures, or not, strongly depends on the study system and the type of organism concerned. Second, there are only a few studies that have used CMR models and have focused on some classes of fitness functions (e.g., fitness functions of behavioral traits).

### 4.2.1 Morphology

Several studies of birds have used CMR estimation models with individual covariates to address selection on body size (wing length), mass, condition in juveniles (e.g., lesser snow goose, Cooch et al. 2002) or adults (tufted duck *Aythya fuligula*, common pochard *Aythya ferina*, and Northern shoveler *Anas clypeata*, Blums et al. 2005), or both (serins *Serinus serinus* Conroy et al. 2002). Body condition can be viewed “as the size of the individual’s energy reserves relative to its body size” (Blums et al. 2005). As migration is demanding in terms of energy, Blums et al. (2005) predicted a positive relationship between survival probability and body condition, but they also considered the possibility for costs associated with very high mass, as did Conroy et al. (2002). Specifically, they considered non-monotonic functions of body condition for survival probability. Both Cooch (2002) and Conroy et al. (2002) found evidence that the relationship between body mass and survival probability varied according to other covariates. Cooch (2002) found evidence of a positive relationship between survival probability and body mass in late-hatched young only. Conroy et al. (2002) found evidence of a negative influence of body mass in years with low density of competitors (siskins; *Carduelis spinus*). That is, in serins the shape of the fitness function varied with environmental conditions (biotic conditions). In lesser snow geese the fitness function differed according to the value of another trait (hatching date), which suggests that selection on body mass cannot be understood without considering the covariance between several traits (e.g., Lande and Arnold 1983; Houle 1991; Pigliucci 2006). The ability to use models including several covariates, both individual and time-specific environmental covariates proved important. Similarly, Wikelski and Trillmich (1997) addressed sex-specific relationships between survival probability, fertility, and body size in Iguanas (*Amblyrhynchus cristatus*; see also Laurie and Brown 1990) and suggested that balanced selective forces shaped body size in this species: sexual

selection favoring large sizes in males in a lek-mating species, but natural selection penalizing large individuals in years with lower resource availability. CMR estimation models have also been used to address micro-evolutionary processes in morphological traits in taxa that are not often mentioned in EURING meetings. For example, Kingsolver and Smith (1995) have addressed wing pattern traits in a butterfly species (*Pontia occidentalis*). They found evidence of a negative influence of mean grey level of the dorsal wing and of ventral hind wings on daily survival. They suggested that this relationship resulted from the influence of color on thermoregulation ability.

Fitness functions based on estimates of survival probability have also been used to address the balance between sexual and natural selection in the wild. For example, Gregoire et al. (2004) have addressed the relationship between bill color in European blackbirds (*Turdus merula*) and survival probability. Theory of sexual selection assumes that there are advantages associated with exaggerated sexual characters in males, more precisely a larger breeding success probability (Andersson 1994). However, there may also be costs associated with secondary sexual traits, such as energetic costs of producing ornaments, increased detectability by predators or intra-specific competition (survival costs). Gregoire et al. (2004) found evidence of stabilizing selection on bill color using models with individual covariates. However, there are several non-exclusive hypotheses concerning the relationship between ornament expression and survival probability. Ornamental traits are assumed to have evolved through mate choice: in birds, individuals with the most showy feathers for example are assumed to be “higher-quality” individuals because they can afford to display costly adornments. In long-lived species, re-mating with the same mate has been shown to have advantages; loss of the mate through mortality may be very costly. Ornaments are assumed to serve as viability indicators: individuals may benefit from choosing a “higher-quality” mate with high survival ability. In this view, one may expect a positive relationship between survival probability and ornament size. Jones et al. (2002) have addressed the relationship between sexually selected feather ornaments and survival probability in crested auklets (*Aethia cristatella*), but have not found evidence of such a relationship. Here again, ultra-structural models were used.

For quantitative traits (as defined in Conner and Hartl 2004, p. 97), the shape of the relationship between fitness and trait values provides insight into the type of phenotypic selection (Conner and Hartl 2004). Directional selection is characterized by a linear fitness function, stabilizing selection by a quadratic function where fitness is highest at some intermediate value of the phenotype, and disruptive selection by a quadratic function where fitness is lowest at some intermediate value of the phenotype. However, as emphasized by Gimenez et al. (2006), the shape of the fitness function estimated using empirical data may not be quadratic, and more complicated forms of selection can occur (Conner and Hartl 2004). There is an analogy between the need for development of relevant fitness functions to address natural selection and the need for development of relevant forms for reproductive or survival functions in optimal control solutions of problems in population dynamics (Runge and Johnson 2002). Gimenez et al. (2006) have developed a nonparametric approach to fitting cubic splines within a CMR framework to address

the relationship between body mass and survival in sociable weavers (*Philetairus socius*). Model parameters were estimated using a Bayesian approach in WinBUGS (Spiegelhalter et al. 1996). They found evidence that the fitness function is not symmetric, which suggests that body mass may not be under stabilizing selection. The technical development in Gimenez et al. (2006) reflects development in quantitative genetics where cubic splines and locally weighted least squares are used to assess the shape of fitness functions (Conner and Hartl 2004).

#### 4.2.2 Behavior

Very few CMR studies have addressed fitness functions of behavioral traits other than those involved in dispersal and breeding activities. The studies I am aware of have investigated the influence of discrete behavioral traits on fitness components. For example, Webb (2006) addressed the consequences of tail autotomy in gekos (*Oedura lesueurii*) on survival probability. Some animals autotomize their tails, which is thought to facilitate escape from predators. Tail autotomy may increase the likelihood of surviving a predator's attack, however, this may have costs including: reduced growth, loss of energy reserves, decreased mating success, loss of social status, and decreased probability of survival during subsequent encounters with predators. Results did not provide evidence that spontaneous tail autotomy influences survival of juvenile geckos.

In a completely different framework, Cam et al. (2002b) have addressed fitness functions of behavior before recruitment: age-specific survival and recruitment probability, and breeding success probability in the first breeding occasion and subsequent occasions. Squatters are individuals present on nesting sites they don't own, containing chicks, when the owners are absent (e.g., during foraging trips at sea). Squatters may be aggressive and even kill the chicks, exhibit territorial behavior and coordination behavior with another squatter of the opposite sex. It has been suggested that squatting is part of behavioral maturation and territory acquisition and may influence age-specific recruitment probability. Results provided evidence that squatters have a higher age-specific local survival and recruitment probability than non-squatters in age-classes where squatting is represented, and a higher breeding success probability than non-squatters at the same age (Cam et al. 2002b). In addition, the relationship between initial breeding success probability and subsequent success probability was addressed using random intercept models (i.e., frailty models): individuals with high initial breeding success probability consistently have higher subsequent success probability. Consequently, it may be relevant to use squatting status before recruitment as a measurable covariate to account for permanent differences among individuals over life (i.e., as an observable criterion to classify individuals in "quality" classes).

### 4.3 Coevolution

Few CMR studies have addressed the evolution of morphological and life history traits within the framework of coevolution. Although morphology and life histories

have been treated above, studies of coevolution are rare and are worth identifying separately. For example, Benkman et al. (2005) addressed bill size and survival probability in red crossbills (*Loxia curvirostra*). Their hypothesis to explain the difference in mean bill size between two populations was local infestation by the scaly-leg mite (*Knemidokoptes jamaicensis*) which favored local selection of smaller-bill birds. Indeed, large-billed males were more likely to exhibit symptoms of ectoparasitic mites. The authors found evidence that infestation by mites was associated with lower survival probability and caused directional selection against larger-billed individuals. In a recent review of dispersal and parasitism, Boulinier et al. (2001) deplored the weakness of the empirical basis in this area of research.

Concerning life history evolution, Dugger and Blums (2001) addressed brood parasitism in ducks using several fitness components – breeding success, recruitment in offspring, and adult survival probability. They conducted an experimental study by adding eggs and ducklings to clutches and broods, and also analyzed a larger observational data set. Their objective was to compare fitness components of parasitized and nonparasitized female common pochard (*Aythya ferina*) and tufted ducks (*Aythya fuligula*). They found that addition of small numbers of eggs to host nests (i.e., simulated parasitism) did not influence host clutch size, host hatching success, or nest success for either species. Parasitism by large numbers of eggs did not influence nest success in pochards, but it did in tufted ducks nests (numbers of eggs = 6 or more). Recruitment probability did not differ between parasitized and nonparasitized nests for either species, and parasitism had no negative effect on adult survival. Dugger and Blums (2001) concluded that moderate levels of parasitism do not have a negative influence on host fitness in these species.

#### **4.4 Evolution of Sex-Ratio**

A topic that has received much attention in studies of human populations is evolution of sex-ratio and its variation, either at birth or in the adult segment of the population (i.e., secondary sex-ratio). This topic has also received much attention in studies of animals (e.g., Nager et al. 1999, Weimerskirch et al. 2005), but in many cases without accounting for incomplete detection of individuals. Sex ratio theory is based on the idea that if the fitness benefits of producing males or females vary with environmental or social conditions, parents should adjust the sex ratio of offspring in a way that maximizes their own fitness. For example, if maternal condition influences survival probability in male and female offspring, the mother should produce offspring whose sex ratio maximizes the mother's fitness.

Empirical tests of hypotheses about adjustment of offspring sex ratio according to environmental and social conditions are scarce. Uller et al. (2004) addressed the influence of pre-natal sex-ratio on offspring survival and adult reproductive parameters in common lizards (*Lacerta vivipara*). In viviparous animals, sex ratio in-utero may influence the characteristics of offspring through exposure to sex-specific steroids in-utero and hormonal interactions between offspring. Evidence from studies in mammals suggests that both sexes are negatively affected by

opposite-sexed siblings. Uller et al. (2004) provided evidence of a long-lasting influence of early conditions on fitness components, more precisely of an influence of pre-natal sex ratio on female fecundity, but not on survival probability. Age at maturity was also influenced by pre-natal sex-ratio. Prenatal sex-ratio may be maladaptive: females from male-biased clutches have lower fecundity and mature earlier than females from female-biased clutches. The fitness return for the mother may not be compromised because negative effects on the underrepresented sex could be counteracted by positive effects on the overrepresented sex. Thus, evolutionary consequences of pre-natal sex ratio on secondary sex ratio are still poorly understood.

#### ***4.5 Movement Among Locations and Habitat Selection Studies***

Development of multistate models (Arnason 1973; Hestbeck et al. 1991; Brownie et al. 1993) also gave an enormous stride to studies of movement, migration and dispersal using data from wild marked animals (Bennetts et al. 2001; Kendall and Nichols 2004). This is one of the topics that have received attention in a large proportion of CMR studies relevant to evolutionary ecology. In a paper focusing on use of multistate models in evolutionary ecology, Nichols and Kendall (1995) laid the foundations of many subsequent studies of movement in subdivided populations (e.g., Spindelov et al. 1995; Senar et al. 2002; Blums et al. 2003, Skvarla et al. 2004). They basically explained in detail the relationship between model parameterization and classical hypotheses put forward in the literature on dispersal. One class of hypotheses considered corresponds to models of gene flow in systems of subdivided populations (e.g., influence of distance among locations on movement probability; Skvarla et al. 2004). In evolutionary ecology, because CMR studies mostly focus on vertebrates (i.e., mobile animals dispersing actively), movement among locations has mostly been addressed within the framework of habitat selection theory (e.g., Fretwell and Lucas 1970).

In long-lived species, it is natural to assume that individuals have to make decisions concerning breeding sites several times during life. When the individual's perspective is considered, the evolution of dispersal can be addressed within the framework of "habitat selection", whose broad scope encompasses both the decision of leaving a site and the choice of a new one (Ronce et al. 2001). Environmental conditions are likely to vary over space and time; for this reason, fixed dispersal strategies are unlikely to be favoured by natural selection (e.g., Ronce et al. 2001). Dispersal can be viewed as a decision making problem (i.e., "to stay or to leave?"; e.g., Danchin et al. 1998; Doligez et al. 1999; Brown et al. 2000; Serrano et al. 2001). It has been hypothesized that decisions are state-specific (i.e., depend on the individual state, such as condition, previous breeding success, breeding habitat, other environmental factors; e.g., Danchin et al. 1998). Recent syntheses about dispersal highlighted the growing attention to questions of individual plasticity and condition-dependant dispersal (Danchin et al. 2001; Ims and Hjermmann 2001; Ronce et al. 2001; Serrano et al. 2001; Serrano and Tella 2003).

A key question is how individuals make decisions concerning fidelity to the previous breeding site, or if they decide to move, selection of a new one. One of the main predictions of the “ideal free habitat selection theory” (Fretwell and Lucas 1970) is that natural selection should favour dispersal tactics where moving leads to increased realized fitness (i.e., habitat selection should be shaped by fitness maximization; Holt and Barfield 2001). Densities in the various locations are expected to change as well as realized fitness in each habitat, and eventually realized fitness is equilibrated. This is why studies based on this theoretical framework do not always address “realized” fitness functions: fitness is not assumed to vary according to behavioral decisions in a systematic manner. The form of the function depends on the state of the study system (e.g., a sub-divided population), whether it is at evolutionary equilibrium, whether fitness is density-dependent, etc. Because of the numerous assumptions this theory relies on (e.g., individuals have perfect knowledge of their environment, there is no cost of moving, etc.; Holt and Barfield 2001), the scenario leading to the “ideal free distribution” of individuals in space developed by Fretwell and Lucas (1970) is unlikely to be observed in the wild (Nichols and Kendall 1995). However, the seminal idea that habitat selection is shaped by fitness maximization leads to some specific predictions that have been tested in several CMR studies of habitat selection. The hypothesis that fitness maximization shapes habitat selection tactics leads to the question of how individuals can assess fitness prospects in different potential locations (Danchin et al. 1998).

For example, it has been hypothesized that individuals use their own breeding success and the success of conspecifics as cues to assess expected location-specific fitness (Danchin et al. 1998; Doligez et al. 1999; Brown et al. 2000; Serrano et al. 2001), and that the decision regarding the location where they will breed in year  $t + 1$  is made based on evidence from year  $t$ . Serrano et al. (2005) suggested that colony size also contributes to determine fitness prospects. Several CMR studies have addressed breeding habitat selection and movement within this framework (e.g., Doligez et al. 2002, 2004; Cam et al. 2004a; Serrano et al. 2003, 2005). In a different vein, Brown et al. (2005) have addressed how intrinsic individual characteristics (more precisely, steroid hormone level and its influence on competitive ability) influenced movement probability among colonies and colony choice in cliff swallows (*Petrochelidon pyrrhonota*).

Furthermore, theories of habitat selection have been invoked to address life history traits other than movement probability per se. Indeed, because the quality of the breeding habitat is likely to influence individual fitness, natural selection may favor habitat selection tactics involving decisions about “when to breed”. It has been suggested that the two decisions “where to breed” and “when to breed” are “two sides of the same coin” (Ens et al. 1995). Habitat selection tactics and age-specific recruitment probability have been addressed in several studies based on CMR data (e.g., Oro and Pradel 2000; Frederiksen and Bregnballe 2001). The evolution of dispersal has also been addressed outside the framework of habitat selection theory. More specifically, it is sometimes assumed that parents produce offspring with fixed dispersal strategies (e.g., philopatric versus dispersing offspring). Within this framework, Hamilton and May (1997) have suggested that in species with

senescent decline in survival, whether parents should produce philopatric versus resident offspring should depend on their age. Few CMR studies have addressed hypotheses about age-specific variation in reproductive investment or reproductive performance, and dispersal (e.g., natal dispersal and senescence; Ronce et al. 1998).

Last, dispersal evolution theories or habitat selection theories make assumptions about whether dispersal is costly (e.g., there may be mortality costs associated with movement, costs of settling because of competition with conspecifics, or costs associated with reproduction in unfamiliar environments). Massot et al. (1994) have studied settlement ability using experimentally translocated common lizards (*Lacerta vivipara*). They compared individuals that survived after the introduction with those of non-manipulated populations. Results provided evidence that translocated individuals had a lower survival probability after being transferred to their new habitat, except juveniles. Adults may thus incur costs associated with unfamiliarity with the new habitat. Selected individuals had particular features in terms of body mass and size. In addition, surviving transplanted males have the same characteristics as transients or immigrants in natural populations (body mass and size); they may thus have been transients or immigrants in their own population of origin. However, this did not hold in females.

## **5 Development of CMR Estimation Models to Address the Genetic Basis of life History Traits in Wild Animal Populations**

A condition for natural selection is heritability in the focal trait (Premise (iii), Section 4.1.). Until now, evolutionary ecologists have used CMR estimation models to address the relationship between demographic parameters themselves (i.e., covariation in life history traits) or between demographic parameters and morphological traits (i.e., fitness functions), which has permitted them to gain insights into Premise (ii) for natural selection. However, studies of Premise (iii) have concerned either “non-demographic” traits (morphological, physiological, behavioral traits), or demographic traits estimated without accounting for imperfect detection of individuals by investigators. As far as the evolution of demographic parameters themselves is concerned, the genetic basis of these traits has not been addressed using CMR estimation techniques. Here I suggest that recent methodological development concerning both quantitative genetics models of estimation of additive genetic variance of traits and CMR models of estimation of demographic parameters theoretically allows integration of the two fields.

### ***5.1 Features of Current Knowledge of Heritability of Demographic Parameters in Wild Animal Populations***

Without using CMR estimation models, several studies have provided evidence that life history traits (fitness components such as age of first breeding, lifetime reproductive success, clutch size or litter size for example) exhibit low heritability

compared to other traits (morphological, physiological or behavioral traits), but the studies in question have also provided evidence that such heritability levels cannot be ignored, and that they vary among species for the same trait and among populations of a single species (Stearns 1992; Matos et al. 1997; Kruuk et al. 2000; Réale and Festa-Bianchet 2000; Réale et al. 2003; Sheldon et al. 2003; Charmantier et al. 2006a, b; Pigliucci 2006). Comparison of results obtained using different statistical techniques to address heritability and additive genetic variance of traits (more precisely parent-offspring regression versus the *animal model*; Section 5.2.2) have provided evidence that the question of heritability of life-history traits should be re-addressed using the most modern techniques (e.g., Kruuk et al. 2001). Moreover, several researchers have pointed out that despite the success of quantitative genetics theory in domesticated animal and plant breeding, very few studies of natural populations have provided evidence of micro-evolutionary changes in heritable traits in response to selection in the presence of directional selection (Kruuk 2004). Two hypotheses have been put forward to explain this: (1) the approaches to estimation of the amount of genetic variation transmitted from parents to offspring we have used so far lead to biased estimates of variation or of the strength of selection (more precisely they overestimate the additive genetic variance or the directional selection differential, (see below)), and (2) the genetic basis of different traits should not be addressed separately (Lande and Arnold 1983; Houle 1991). Researchers in quantitative genetics have developed approaches to estimating genetic parameters that may partly solve these problems (Lynch and Walsh 1998).

Importantly, the problem of imperfect detection of individuals by investigators has been overlooked. Until now, in wild animal populations, quantitative genetics studies focusing on demographic parameters have been conducted using observed values of life-history traits (e.g. Sheldon et al. 2003), which is reasonable only in situations where detection probability of marked individuals alive and present in the study area is close to 1. Such situations have long been known to be rare in wild animal populations (Lebreton et al. 1992; Clobert 1995; Martin et al. 1995). In the vast majority of populations, estimation of survival or dispersal probability, age-specific recruitment probability (one definition of which is the probability of making a transition between state “pre-breeder” and state “breeder” at a given age), and adult breeding probability (in species exhibiting intermittent breeding), all require use of estimation models explicitly incorporating detection probability. Unless this probability is equal to 1, the age at which the first breeding event was recorded cannot be assumed to be a reliable measure of age of recruitment, and the age at which the last breeding event was observed cannot be assumed to be a reliable measure of age of last reproduction, observed breeding events cannot be assumed to account for all the breeding attempts in an individual’s life, and individuals not recaptured or not resighted in a given year cannot be assumed to be dead that year. In addition, estimation of breeding success probability in a given breeding occasion, the probability of laying a clutch of a given size, or giving birth to a litter of a given size, may require CMR estimation models accounting for state-specific detection probability (i.e., multistate models, Nichols et al. 1994; Nichols and Kendall 1995; Williams et al. 2002). Besides, even if heritability of survival probability per se is

not of interest, in several classes of CMR models for open populations, several of the aforementioned demographic parameters are conditional on survival probability over one or several time intervals between sampling occasions. Therefore, the issue of estimation of survival probability in situations where detection probability is  $< 1$  cannot be ignored.

## ***5.2 Mixed CMR Models to Address Heritability of Demographic Parameters***

Lynch and Walsh (1998, p. 50) summarized the problem of analysis of the genetic basis of quantitative traits as follows: “inferences concerning the genetic basis of quantitative traits can be extracted from phenotypic measures of resemblance between relatives”. Obviously, to use CMR statistical techniques to estimate parameters relevant to quantitative genetics, CMR data from marked *relatives* are needed. Long-term monitoring programs of marked individuals in wild animal populations have often led to such data. The principles of quantitative genetics are general; they have been widely used in animal and plant breeding and are valid in wild organism populations as well. However, “because the systems of mating and evolutionary forces found in natural populations are generally quite different than the controlled programs imposed on domesticated species, study of the inheritance of quantitative traits in natural populations presents a number of challenges” (Lynch and Walsh 1998, p. 5). The distinctive feature of the data sets from wild animal populations is that they correspond to complex pedigrees; there is a variety of degrees of relatedness between individuals. In domesticated animals, investigators design experiments to address the genetic basis of phenotype. In wild animal populations fathers of individuals often cannot be identified unless molecular approaches are used (Thomas et al. 2002), especially in species without paternal care or species where extra-pair paternity is common. Most long-term monitoring programs are purely observational if the target species is protected or is (locally) of conservation concern. Consequently, specific sources of phenotypic variation in populations have seldom been addressed using experimental approaches. Experiments have sometimes been conducted (e.g., cross-fostering, Wiggins 1989), but designs specifically relevant to quantitative genetics are rare and such experiments are usually short term.

One of the main obstacles encountered by researchers using CMR estimation methods to address heritability in demographic parameters is obtaining “one” estimate (“one measurement”) of the focal trait per individual (even the mean value over the lifetime). Early efforts to assess heritability in quantitative traits (morphological traits or life history traits) have relied on estimation of the slope of parent-offspring regression (Lynch and Walsh 1998), which requires one measurement of the trait in parents (or one parent) and one measurement in offspring. This was done either by estimating the mean value of the trait over the parent’s lifetime and the mean value of the offspring trait over its lifetime, or by taking one single measurement of the parent and the offspring. Approaches to estimation of demographic

parameters almost inevitably involve some degree of aggregation of data (Cooch et al. 2002; Nichols 2002), and it is not possible to estimate quantities like “the individual survival probability” using data from a single individual. Development of models with individual covariates (Skalski et al. 1993) allows investigators to achieve high levels of stratification of populations (Cooch et al. 2002) and to estimate individual-specific demographic parameters (e.g., an “individual survival probability”), provided relevant measurable covariates are available. However, the distribution of the focal trait (the individual survival probability) in the population may not be accounted for in a satisfactory manner by the relationship between survival probability and a measurable individual covariate (e.g., body size, laying date in birds, etc.).

Recent developments in CMR estimation methods share a common feature with the most recent techniques to estimate heritability (Fry 1992; Lynch and Walsh 1998; Kruuk 2004; Schaeffer 2004), namely, use of mixed models (including both fixed and random effects). More specifically, the feature shared by the *animal model* in quantitative genetics and some CMR estimation models is that part of the variation in the focal trait is accounted for by random effects. As emphasized in Section 4.1.2, in human demography, random effects have long been used to account for individual heterogeneity in mortality risk. Mixed effects models may not provide investigators with “one estimate of survival probability per individual”, but they provide an estimated distribution of the demographic parameter in the population, that is, an estimated variance of the focal trait among individuals (after accounting for relevant fixed effects: sex, age, location, etc.). Similarly, according to Kruuk (2004) “One of the major recent changes in the study of quantitative genetics of natural populations has been the use of mixed models, in particular the form of mixed models known as the ‘animal model’, for the estimation of variance components.”

The following section is largely inspired by Lynch and Walsh (1998), and Conner and Hartl (2004): it is intended for readers without background in quantitative genetics. This material is needed to understand the points shared by recently developed CMR and quantitative genetics estimation techniques. All the topics addressed here are extensively covered in two quantitative genetics “bibles” (Falconer and Mackay 1996; Lynch and Walsh 1998).

### 5.2.1 A Very Short Introduction to Quantitative Genetics Theory

The *phenotypic value* of an individual (the measurement of a given quantitative trait for an individual: morphological, demographic, physiological, or behavioral trait),  $z$ , is determined by the individual genotype and the environment. Quantitative genetics “focuses on the phenotype, usually without knowing the genotype underlying the traits” (Conner and Hartl 2004, p. 3). The traits “are encoded by a large number of genetic loci, and for practical reasons, the individual loci are generally unobservable” (Lynch and Walsh 1998, p. 4). The phenotypic value is assumed to be the sum of the total effects of all loci on the trait,  $G$ , the *genotypic value* and an *environmental deviation*  $E$ . That is,

$$z = G + E \tag{1}$$

The genotypic value is the phenotype produced by a given genotype averaged across environments. The environmental deviation is the difference between the phenotypic and the genotypic values caused by the environment (temperature, prey availability, rainfall etc., Conner and Hartl 2004, p. 101). The mean and the variance ( $\sigma_p^2$ ) characterizing the distribution of individual phenotypic values are properties of populations; there is a distribution of individual genotypic values and of individual environmental deviations. The distribution of environmental deviations is generally assumed to be normal with mean = 0. One central goal of quantitative genetics is partitioning the phenotypic variance  $\sigma_p^2$  into genetic and non-genetic components:

$$\sigma_p^2 = \sigma_G^2 + \sigma_E^2 \quad (2)$$

where  $\sigma_G^2$  is the genotypic variance and  $\sigma_E^2$  is the environmental variance.

The evolutionary response of a trait to selection is a function of the intensity of selection and the fraction of the phenotypic variance attributable to certain genetic effects (Lynch and Walsh 1998). More specifically, one draws a distinction between *additive genetic effects* (the effects of each allele in the genotype adds to determine the total effect on the phenotype) and interactions between alleles at the same locus, *dominance*, or at different loci, *epistasis*. Hence, the genotypic variance  $\sigma_G^2$  can be partitioned into  $\sigma_A^2$ , the additive genetic variance,  $\sigma_D^2$  the dominance variance, and  $\sigma_{EPI}^2$ , the epistatic variance (or interaction). That is,

$$\sigma_G^2 = \sigma_A^2 + \sigma_D^2 + \sigma_{EPI}^2 \quad (3)$$

The additive genetic variance is the most important for sexually reproducing species because only the additive effects of genes are transmitted directly from parents to offspring; information on other sources of genetic variation (e.g., linkage disequilibrium, polyploidy, etc.) can be found in Lynch and Walsh (1998).

The directional selection differential,  $S$ , is the within-generation difference between the mean phenotype after an episode of selection (but before reproduction) and the mean before selection. Because of direct transmission of additive effects,  $\sigma_A^2$  is most important in determining changes in mean phenotypic values across generations in sexual species. It is also the easiest of the genetic components of variance to estimate using resemblance between relatives: resemblance is caused primarily by additive variation (Lynch and Walsh 1998). Change in mean phenotypic values across generations is the definition of phenotypic evolution (Deduction II). The degree to which the mean phenotype after selection  $\mu_s$  deviates from the mean before selection  $\mu_0$  depends on survival probability and reproduction (fitness) of individuals with different phenotypes. Under specific assumptions concerning the (un-) importance of genotype  $\times$  environment covariance and interaction, if the regression of the offspring phenotype on that of its average parent is linear with slope  $\beta$ , a change in the parental mean phenotype induces an expected change in the mean phenotype across generations equal to:

$$\Delta\mu = \mu_0 - \mu_s = \beta^*S. \quad (4)$$

where  $\mu_0$  is the mean phenotype of the offspring of the selected parents. This equation is the *breeder's equation*. "It combines information on the forces of selection (S) with that on inheritance ( $\beta$ ) to yield a predictive equation for evolutionary change across generations. If  $\beta$  is zero, no matter how large S is, the response to selection across generations is zero" (Lynch and Walsh 1998, p. 47).

In sexually reproducing species, genotypes are not passed on from parents to offspring, but are created anew in each offspring by combining an allele from each parent at each locus. "The breeding value can be defined as the effect of an individual's genes on the value of the trait in its offspring; this effect is caused by the additive effects of genes – it is sometimes called 'additive genotype' and has variance"  $\sigma_A^2$  (Conner and Hartl 2004, p. 111). Heritability is the proportion of the phenotypic variance that is due to genetic causes. Broad-sense heritability is defined as follows:

$$H^2 = \frac{\sigma_G^2}{\sigma_P^2} \quad (5)$$

However, because the genotypic value includes genetic components (e.g., epistasis) that do not contribute to resemblance between relatives as much as the additive genetic component, we usually define the narrow-sense heritability:

$$h^2 = \frac{\sigma_A^2}{\sigma_P^2} \quad (6)$$

In parent-offspring regression,  $h^2$  can be estimated using the slope of the regression.

### 5.2.2 The Classical Parent-Offspring Regression and the Animal Model

Parent-offspring regressions involve measurements from individuals with specific degrees of relatedness. This commonly used technique to estimate heritability has advantages that are not restricted to practical considerations (such data are usually available and the computations are done using classical least squares regression): parent-offspring regression is not affected by dominance or linkage (loci close together on the chromosome are said to be genetically linked, which makes recombination between loci during meiosis rarer; see Lynch and Walsh 1998 for details, p. 537). However, in monitoring programs of wild animal populations, information from individuals with different degrees of relatedness is available. The so called *animal model* allows investigators to make full use of the available information. The fact remains that the degree of relatedness of the individuals included in the analysis must be known, and the corresponding information is used in a model where phenotypic values are expressed as a function of fitness, breeding values, environmental effects, etc.

In addition, in parent-offspring regression, measurements from individuals were either averaged over life, or a single observation was retained for analysis. For some traits, lack of variation over life may be a reasonable assumption (e.g., body size

after sexual maturity in species whose growth takes place before reproduction), but not for all traits (e.g., clutch size in birds) or all species (e.g., body size in snakes). Last, genotype  $\times$  environment covariance and interactions are assumed to be negligible, as well as permanent maternal effects if data from the sole mother are available (permanent maternal effects occur when the phenotype of the offspring is influenced by the phenotype of the mother, which may be caused either by genetic or environmental effects; Mousseau and Fox 1998). One of the advantages of the *animal model* is to allow investigators to take such effects into account explicitly in analyses of phenotypes to address variance components and heritability. Studies that have used both parent-offspring regression and the *animal model* with the same data set to address heritability have often provided evidence of discrepancies in results (e.g., Kruuk et al. 2001), which may result from the fact that variance components accounting for a larger number of sources of variation in phenotypic values can be included in analyses with the *animal model* compared to parent-offspring regression (Kruuk 2004).

### 5.2.3 Estimation of Heritability and Breeding Values: The Animal Model

#### General Formulation of the Animal Model

For the sake of simplicity, here I will assume that phenotypic values of a trait (morphological, physiological, behavioral, or demographic) are normally distributed, as in the case in many quantitative genetics applications (when focusing on traits such as body mass, size, or laying dates in birds for example; e.g., Kruuk et al. 2000; Wilson et al. 2005). However, the statistical theory for estimation of variance components and prediction of random effects in mixed models exists for variables with other distributions (e.g., Bernoulli, Poisson; Fahrmeir and Tutz 1994; Matos et al. 1997; Lynch and Walsh 1998, p. 745, 779), which may be more useful for addressing heritability in traits such as survival probability or breeding success probability. Besides, estimation per se is beyond the scope of this paper: several approaches have been developed in quantitative genetics (namely, REML and Bayesian methods based on Markov Chain Monte Carlo simulations; Blasco 2001), which are well suited for complex pedigrees with unbalanced data, as is usually the case in long-term monitoring programs of wild marked animal populations. These methods can be implemented within the framework of CMR estimation models (e.g., Dupuis 1995; Dupuis et al. 2002; Vounatsou and Smith 1995; Royle and Link 2002; Brooks et al. 2002, 2004; King and Brooks 2002, 2004; Link and Barker 2004; Otis and White 2004; Royle 2007; Royle and Kéry 2007). However, to estimate heritability in fitness components, more flexible mixed CMR models than existing models are needed.

In the general case (i.e., where the phenotype is determined by genetic and environmental effects plus interactions between them), the phenotype of the  $k$ th individual of the  $i$ th genotype exposed to the  $j$ th environmental effect can be described as a linear function of four components (Lynch and Walsh 1998).

$$z_{ijk} = G_i + I_{ij} + E_j + e_{ijk} \quad (7)$$

where  $G_i$  is the genotypic value, which may be a function of the population mean phenotype (e.g.,  $z$  may depend on age, year of birth, gender for example, which can be accounted for using additional fixed effects, and year using either fixed or random effects, depending on the study).  $G_i$  includes the additive genetic effects (breeding value) and possible genetic components such as dominance and epistasis (different gene effects on the phenotype).  $E$  is the environmental effect on the phenotype,  $I$  is the genotype  $\times$  environment interaction effect on the phenotype, and  $e$  is the residual deviation.

Accordingly, the total phenotypic variance of a population can be written as:

$$\sigma_P^2 = \sigma_G^2 + \sigma_I^2 + 2\sigma_{G,E} + \sigma_E^2 + \sigma_e^2 \quad (8)$$

where  $\sigma_{G,E}$  is the genotype  $\times$  environment covariance.  $\sigma_I^2$  is the genotype  $\times$  environment interaction, which corresponds to the variation in the phenotypic response of specific genotypes to different environments.  $\sigma_{G,E}$  is the physical association of specific genotypes with environments: if the genotypes are randomly distributed with respect to environment,  $\sigma_{G,E}$  is zero.  $\sigma_G^2$  may be further decomposed according to additive genetic variance ( $\sigma_A^2$ ) and types of gene effects on the phenotype (see above). A source of environmental variation of particular interest in evolutionary ecology is maternal effects (for additional information, see Lynch and Walsh 1998).

A distinctive feature of the *animal model* is that random effects are used to account for the additive genetic variance (breeding values), and that information on the degree of relatedness of the individuals included in the analysis is used to estimate  $\sigma_A^2$ . Other random effects may be used to account for other components of the genotypic value (e.g., genotype  $\times$  environment covariation), and also to account for sources of variation in the phenotypic values other than genetic effects (e.g., environmental effects). The general formulation of the *animal model* is the following. Consider a  $n \times 1$  column vector  $y$  with  $n$  observed phenotypic values. The model assumes that  $y$  can be described as a linear model with a  $p \times 1$  vector of  $p$  levels of fixed effects ( $\beta$ ), a  $q \times 1$  vector of  $q$  levels of random effects ( $u$ ), and an  $n \times 1$  vector of random, residual terms ( $e$ ). The first element of vector  $\beta$  is generally the population mean. Importantly, the elements of the vector  $u$  are usually genetic effects, including additive genetic effects (i.e., breeding values). The residual deviations are assumed to be independent of random genetic effects.

$$y = X\beta + Zu + e \quad (9)$$

$X$  and  $Z$  are design matrices whose elements are equal to 0 or 1 depending on whether the effect influences the individual's phenotype. The expectation of  $y$  is:

$$E \begin{pmatrix} y \\ u \\ e \end{pmatrix} = \begin{pmatrix} X\beta \\ 0 \\ 0 \end{pmatrix} \quad (10)$$

and the variance–covariance structure of  $y$  is:

$$V \begin{pmatrix} u \\ e \end{pmatrix} = \begin{pmatrix} G & 0 \\ 0 & R \end{pmatrix} \quad (11)$$

$G$  is the variance–covariance matrix for random effects other than residual terms, and  $R$  is the variance–covariance matrix of residuals. The square matrices  $G$  and  $R$  are assumed to be non-singular and positive definite.  $V$  is usually expressed as follows:

$$V = V(y) = ZGZ' + R \quad (12)$$

In many applications, residual terms are assumed to be independently and identically distributed with mean 0 and variance  $\sigma_e^2$ . Therefore,  $R = I\sigma_e^2$ . In situations where the phenotype is assumed to be completely influenced by fixed effects (e.g., age), and observations are independent (e.g., there is only one observation per individual),  $V$  is equal to  $R$ . However, the distinctive feature of genetic analysis is that  $V$  is generally not diagonal. By definition, individuals with some degree of relatedness share part of their genes and the main objective of quantitative genetics analysis is to address the genetic basis of phenotype using resemblance between relatives. Hence, it is hypothesized that the phenotypic values of relatives are not independent and that part of the dependence is caused by additive genetic effects: addressing this hypothesis is central to quantitative genetics.

### Incorporation of Dependency Among Relatives in CMR Models

The matrix  $G$  describes the covariance among random effects. Assuming that the only random effects ( $u$ ) in the model are the additive genetic effects,  $G$  corresponds to the covariance in additive genetic effects among relatives. It can be shown that the covariance between two relatives  $i$  and  $j$  is given by  $2\Theta_{ij}\sigma_A^2$ , where  $\Theta_{ij}$  is the coefficient of coancestry (Falconer and Mackay 1996, Lynch and Walsh 1998). It is the probability that an allele drawn at random from individual  $i$  will be identical by descent to an allele drawn at random from individual  $j$ . For example, this probability is 0.25 for parent and offspring, so that the additive genetic covariance between them is  $0.5\sigma_A^2$  (Kruuk 2004). The matrix including (twice the) coefficients of coancestry must be built before the analysis (it is often called the *Numerator Relationship Matrix*,  $A$ ), according to the specific data set in hand and the corresponding pedigree. Several pieces of software or routines have been designed to build it (e.g., Kruuk 2004, Saxton 2004, Kinghorn and Kinghorn 2007). This matrix is used to specify the variance–covariance structure of  $u$ :  $G$ .  $R$  and  $G$  have to be modified according to the design of the study and the question addressed. For example, their structure may account for repeated measures from the same individual through an additional random effect reflecting permanent environmental effects on all observations from the same individual, and through non-independence of residual terms (Kruuk 2004). Similarly, maternal effects or common environmental effects can be

accounted for by an additional random effect on all offspring of a given mother, or on all individuals sharing the same environment during development, respectively.

Recently developed CMR models designed to estimate demographic parameters allow consideration of both fixed and random effects. Importantly, development of individual-level models to accommodate individual covariates (Skalski et al. 1993; Royle 2008) required specification of the likelihood for each individual capture–recapture history; this is also required to accommodate individual random effects (Royle 2007). Incorporation of a user-defined design matrix and variance–covariance matrix for random effects is what remains to be made possible to address the genetic basis of demographic parameters estimated using CMR estimation models accounting for incomplete detection of individuals. It is important to note that in quantitative genetics, the assumption of non-independence among individuals is central: the main objective of analyses is assessment of the contribution of common genetic material to resemblance among relatives. Therefore, development of flexible tools to specify the variance-covariance matrix of random effects will probably greatly influence the success of the efforts to address heritability in demographic parameters.

### Multitrait Models

The *animal model* has been used in quantitative genetics to conduct multivariate analyses of life history traits (Charmantier et al. 2006a). The “multivariate breeder’s equation” (Pigliucci 2006) allows consideration of pleiotropic effects such as antagonistic pleiotropy invoked in evolutionary theories of aging (e.g., Tatar 2001). In theory, the state-space formulation of the Arnason–Schwarz model for example allows simultaneous estimation of several life history traits. Several individual random effects can be used (Yashin et al. 2002; Cam et al. 2004b) to address the correlation in latent life history traits.

### Other Methodological Challenges

In addition to the technical difficulties associated with the specification of a user-defined variance–covariance matrix for random effects in CMR estimation models, two other issues will require additional efforts. First if estimation is done within the Bayesian framework, according to some researchers, how to conduct model selection is unclear for models with random effects (e.g., Spiegelhalter et al. 2002). Some computer-intensive methods (Reversible Jump Markov chain Monte Carlo simulations; Green 1995) have been proposed to explore variable dimension statistical models, but may be difficult to implement in a flexible manner in standard software programs (Brooks et al. 2002). In addition, there has been a strong emphasis on evaluation of the fit of models using information criteria to perform model selection (e.g., Lebreton et al. 1992; White 2002; Choquet et al. 2003; Pradel et al. 2003). Here again, how to assess the fit of models is not straightforward.

## Breeding Values and Selection Studies

As emphasized above, studies involving CMR models to estimate demographic parameters have addressed the question of the evolution of morphological or physiological traits using fitness functions: the relationship between the phenotypic value of a (morphological, physiological, behavioral) trait and fitness components. Kruuk (2004) pointed out that one may find evidence of such a relationship even in situations where there is no relationship between the genetic basis of the trait and fitness. This may occur when there is an environment-induced covariance between the trait and fitness (variation in environmental conditions are associated with joint variation in trait values and fitness). To detect such a phenomenon, the *animal model* may be used to predict individual breeding values (i.e., prediction of an individual random effect accounting for  $\sigma_A^2$ , the variance of the additive genotype). Comparisons between two ways of assessing selection gradients provide insight into the above covariance: fitness functions obtained using breeding values, and using phenotypic values.

### 5.3 Concluding Remarks

As emphasized by Lynch and Walsh (1998), evolutionary biology has considerably been influenced by quantitative genetics, but the need for statistical tools (more specifically, mixed models) to analyze complex pedigrees in wild animal populations is currently one of the motivations for statisticians developing methods to estimate relevant quantities in quantitative genetics. The material introduced above suffers from the simplifying assumptions early quantitative genetics suffered from, but the current machinery of the field and of statistics can handle more complex situations likely to be relevant to wild animal populations, such as genotype  $\times$  environment interactions, maternal, or family effects (e.g., Massot and Clobert 2000). In addition, multivariate phenotypes and pleiotropic effects can be addressed, and a few studies conducted using empirical data from wild animal populations where detection probability of individuals is high have provided evidence of additive genetic variation in life history traits, and of evolutionary trade-offs and opposing directional selection on traits (e.g., Charmantier et al. 2006a).

One should keep in mind, however, that if fitness functions (common in CMR evolutionary ecology studies) are not sufficient to address evolutionary change in traits, quantitative genetics has its limitations as well. Pigliucci (2006, p. 5) recently pointed out that heritability is a “local measure, meaning that it can, and often does, change with changes in the population’s gene frequencies and environments encountered. [. . .] Evolution de facto changes gene frequencies. [. . .] Heritabilities do not provide a useful measure of the long-term capability of traits to respond to selection”. Quantitative genetics is successful at making short-term predictions, mostly qualitative predictions, but in its current state evolutionary biology theory is unable to predict long-term evolutionary change in traits.

In addition, there is a long tradition of experimentation in quantitative genetics, which uses creation of “artificial sets of offspring derived from carefully designed

crosses among parents sampled at random from a natural population” (Pigliucci 2006, p. 9). Experimentations of that type may be possible in some wild animal populations, but long-term studies (e.g.,  $\approx 30$  years) resulting in complex pedigrees haven’t been designed that way. This implies that some inferences (about maternal effects for example) may not be possible with data from wild animal populations. In addition, complex pedigrees may lead to situations where there are small sample sizes to estimate some variance components (Quinn et al. 2006). However, Pigliucci (2006, p. 9) also questioned whether an artificially created set of genotypes should be used to draw inference about genetic parameters in the natural population, because “it is vanishingly unlikely that the individuals in the population in question would ever cross in even approximately the same pattern as required by statistics tests and laboratory experiments”. In other words, the corresponding estimated genetic parameters may not be thought of as the parameters in the natural population.

Nevertheless, limitations of the inferences that can be drawn from quantitative genetics parameter estimates should not overshadow the weakness of our knowledge of heritability of life history traits and of their genetic basis in wild animal populations. As emphasized above, the emergence of new statistical tools calls for studies of the genetic basis of these traits (Kruuk 2004). In addition, the rare studies where detection probability is likely to be high (although not formally estimated) and that have used *animal models* with values of life history traits directly observed (e.g., the mute swan, *Cygnus olor*, population in Abbotsbury, Dorset, U.K.) have provided stimulating results (Charmantier et al. 2006a, b). Last, Houle (1992) pointed out that many previous inferences about the potential for evolution of life history traits compared to other traits have been drawn using narrow-sense heritability,  $h^2$  (see above). Lower heritability of life history traits compared to others has been interpreted as evidence of lower genetic variation in demographic parameters than in other traits. However, Houle (1992) argued that heritability is not appropriate for comparative studies of genetic variation in traits and proposed a dimensionless criterion for this purpose. This also calls for new studies of the genetic basis of life history traits in wild animal populations.

## 6 Additional Topics

“Evolutionary ecologists consider both historical and contemporary influences on patterns of variation and study variation at all levels, from within-individual variation (e.g., ontogenetic, behavioral) to variation among communities or major taxonomic groups” (Fox et al. 2001, Preface). The enormous range of questions potentially relevant to evolutionary ecology is reflected in the explosion of studies that have used CMR estimation models, and of the scope of such models. In this paper, for the sake of conciseness and homogeneity, several important topics and CMR models have not been addressed. One of the reasons for this choice is that overall, studies relevant to evolutionary ecology that have used these approaches are still rare. However, as for models developed earlier, evolutionary

ecologists may only grab these tools once they are widely used elsewhere and are sufficiently developed and flexible to allow them to address novel questions relevant to current evolutionary theory, concepts and methods. There is no conceptual reason why such models should not be used by evolutionary ecologists in the near future.

- (i) CMR approaches to estimation of vital rates specific to ecological communities (e.g., Nichols et al. 1998a, b; Dupuis and Joachim 2006; Kéry and Royle 2008, this volume). These approaches use the species ID as the individual mark in population modelling. A few studies have opened the way to questions undoubtedly anchored in evolutionary ecology. For example, Doherty et al. (2003) have addressed the relationship between sexual selection and local extinction probability in bird communities. As Stenseth and Saetre (2003, p. 5576) emphasized: “community ecology and evolutionary ecology have in the past, to a large extent, been moving along separate paths. [. . .]. However, CMR estimation methods have already been used to draw inferences about variation in species diversity at long evolutionary time scales (Nichols and Pollock 1983). Stenseth and Saetre (2003, p. 5577) also emphasized that “Doherty et al. (2003) provide an excellent demonstration of the potential power of using long-term ecological monitoring data to address key problems in community ecology and evolution”
- (ii) Occupancy estimation models (MacKenzie et al. 2006). This recent book by MacKenzie and colleagues focuses on estimation methods to address “occupancy in ecological investigations”, either occupancy of sampling units by one species, or by several. In other words, these methods are relevant not only to ecological communities (see above), but also to all the studies using “presence–absence data” over space and time for a given species. The number of questions relevant to evolutionary ecology that can be addressed using these methods is very large (e.g., metapopulation dynamics, changes in geographical range, epidemiology). This is an area of active research to develop models to estimate spatio-temporal variation in occupancy probability, but to date mostly methodological work as been done (e.g., MacKenzie and Kendall 2002; MacKenzie et al. 2002, 2004; MacKenzie and Bailey 2004; MacKenzie and Nichols 2004; Royle et al. 2005).
- (iii) Noninvasive genetic sampling. Despite the intensive use of molecular markers in evolutionary ecology (e.g., Conner and Hartl 2004), capture–recapture analysis of DNA-based data has received little attention in this field. Recent development in capture–recapture theory designed for molecular markers may open the way to new studies (Lukacs and Burnham 2005; Petit and Valière 2006).

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## References

- Andersson M (1994) Sexual selection. Princeton University Press, Princeton, New Jersey, U.S.A.
- Anderson DR, Cooch EG, Gutiérrez RJ, Krebs CJ, Lindberg MS, Pollock KH, Ribic CA, Shenk TM (2003) Rigorous science: suggestions on how to raise the bar. *Wildlife Society Bulletin* 31: 1–10.
- Arnason AN (1973) The estimation of population size, migration rates and survival in a stratified population. *Research in Population Ecology* 15: 1–8.
- Arnason AN, Schwarz CJ, Boyer G (1998) POPAN 5: a data maintenance and analysis system for mark–recapture data. Scientific Report, Department of Computer Science, University of Manitoba, Winnipeg. Available at <http://www.cs.umanitoba.ca/~popan>
- Barbraud C, Weimerskirch H (2005) Environmental conditions and breeding experience affect costs of reproduction in blue petrels. *Ecology* 86: 682–692.
- Beauplet G, Barbraud C, Dabbin W, Küssener C, Guinet, C (2006) Age–specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* 112: 430–441.
- Benkman CW, Colquitt JS, Gould WR, Fetz T, Keenan PC, Santisteban L (2005) Can selection by an ectoparasite drive a population of crossbills from its adaptive peak? *Evolution* 59: 2025–2032.
- Bennett PM, Owens IPF (2002) Evolutionary ecology of birds. Oxford University Press, Oxford.
- Bennetts RE, Nichols JD, Lebreton J–D, Pradel R, Hines JE, Kitchens WM (2001) Methods for estimating dispersal probabilities and related parameters using marked animals. In: Clobert J, Danchin E, Dhondt A, Nichols JD (eds), *Dispersal*, Oxford University Press, Oxford, U.K., pp 5–17.
- Blasco A (2001) The Bayesian controversy in animal breeding. *Journal of Animal Science* 79: 2023–2046.
- Blums P, Nichols JD, Lindberg MS, Hines JE, Mednis A (2003) Estimating natal dispersal movement rates of female European ducks with multistate modeling. *Journal of Animal Ecology* 72: 1027–1042.
- Blums P, Nichols JD, Hines JE, Lindberg MS, Mednis A (2005) Individual quality, survival variation and patterns of phenotypic selection on body conditions and timing of nesting in birds. *Oecologia* 143: 365–376.
- Bonner SJ, Schwarz CJ (2004) Continuous time–dependent individual covariates and the Cormack–Jolly–Seber model. *Animal Biodiversity and Conservation* 27: 149–155.
- Boulinier T, McCoy KD, Sorci G (2001) Dispersal and parasitism. In: Clobert J, Danchin E, Dhondt A, Nichols JD (eds), *Dispersal*, Oxford University Press, Oxford, U.K., pp 169–179.
- Brommer JE, Merillä J, Kokko H (2002) Reproductive timing and individual fitness. *Ecology Letters* 5: 802–810.
- Brooks SP, Catchpole EA, Morgan BJT, Harris M (2002) Bayesian methods for analysing ringing data. *Journal of Applied Statistics* 29 (Special Issue): 187–206.
- Brooks SP, King R, Morgan BJT (2004) A Bayesian approach to combining animal abundance and demographic data. *Animal Biodiversity and Conservation* 27: 515–529.
- Brown CR, Bromberger M, Danchin E (2000) The effect of conspecific reproductive success on colony choice in cliff swallows. *Journal of Animal Ecology* 69: 133–142.
- Brown CR, Bromberger M, Brown, Raouf SA, Smith LC, Wingfield JC (2005) Steroid hormone levels are related to choice of colony size in cliff swallows. *Ecology* 86: 2904–2915.
- Brownie C, Hines JE, Nichols JD, Pollock KH, Hestbeck JB (1993) Capture–recapture studies for multiple strata including non–Markovian transitions. *Biometrics* 49: 1173–1187.

- Bryant MJ, Reznick D (2004) Comparative studies of senescence in natural populations of guppies. *American Naturalist* 163: 55–68.
- Burnham KP (1993) A theory for combined analysis of ring recovery and recapture data. In: Lebreton J-D, North PM (eds) *The use of marked individuals in the study of bird population dynamics*, Birkhauser, Basel, pp 199–213.
- Burnham KP, Rexstad EA (1993) Modeling heterogeneity in survival rates of banded waterfowl. *Biometrics* 49: 1194–1208.
- Burnham KP, White GC (2002) Evaluation of some random effects methodology applicable to bird ringing data. *Journal Applied Statistics* 29 (Special Issue): 245–264.
- Cam E, Hines JE, Monnat J-Y, Nichols JD, Danchin E (1998) Are nonbreeders prudent parents? The Kittiwake model. *Ecology* 79: 2917–2930.
- Cam E, Link WA, Cooch EG, Monnat J-Y, Danchin E (2002a) Individual covariation in life history traits: seeing the trees despite the forest. *American Naturalist* 159: 96–105.
- Cam E, Cadiou B, Hines JE, Monnat J-Y (2002b) Influence of behavioural tactics on recruitment and reproductive trajectory in the kittiwake. *Journal of Applied Statistics* 29 (Special Issue): 163–186.
- Cam E, Monnat J-Y, Hines JE (2003) Long-term consequences of early conditions in the kittiwake. *Journal of Animal Ecology* 72: 411–424.
- Cam E, Oro D, Pradel R, Jimenez J (2004a) Assessment of hypotheses about dispersal in a long-lived seabird using multistate capture-recapture models. *Journal of Animal Ecology* 73: 723–736.
- Cam E, Monnat J-Y, Royle JA (2004b) Dispersal and individual quality in a long-lived species. *Oikos* 106: 386–398.
- Cam E, Cooch EG, Monnat J-Y (2005) Earlier recruitment or earlier death? On the assumption of homogeneous survival in recruitment studies. *Ecological Monographs* 75: 419–434.
- Carothers AD (1973) Capture–Recapture methods applied to a population with known parameters. *Journal of Animal Ecology* 42: 125–146
- Caswell H (2001) *Matrix population models*. Construction, analysis, and interpretation. Sinauer Associates, Sunderland, Massachusetts.
- Charmantier A, Perrins C, McCleery RH, Cheldon BC (2006a) Quantitative genetics of age at reproduction in wild swans: support for antagonistic pleiotropy models of senescence. *Proceedings of the National Academy of Sciences of the U.S.A.* 103: 6587–6592.
- Charmantier A, Perrins C, McCleery RH, Cheldon BC (2006b) Evolutionary response to selection on clutch size in a long-term study of the mute swan. *American Naturalist* 167: 453–565.
- Charlesworth B (1994) *Evolution in age-structured populations*. Cambridge University Press, Cambridge.
- Choquet R, Reboulet AM, Pradel R, Gimenez O, Lebreton J-D (2003) *U-Care user's guide*, Mimeographed document, CEFE/CNRS, Montpellier, France. Available at: <ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/>
- Clobert J, Lebreton JD (1985) Dependence de facteurs du milieu dans les estimations de survie par capture–recapture. *Biometrics* 41: 1031–1037. SURGE is available at :<http://ftp.cefe.cnrs.fr/biom/Archives/>
- Clobert J (1995) Capture–recapture and evolutionary ecology: a difficult wedding? *Journal of Applied Statistics* 22: 989–1008.
- Clobert J (2002) Capture–recapture and evolutionary ecology: further comments. *Journal of Applied Statistics* 29 (Special Issue): 53–56.
- Conner MM, White GC (1999) Effects of individual heterogeneity in estimating the persistence of small populations. *Natural Resource Modeling* 12: 109–127.
- Conner JK, Hartl DL (2004) *A primer of ecological genetics*. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.
- Conroy MJ, Senar JC, Domènech J (2002) Analysis of individual- and time-specific covariate effects on survival of *Serinus serinus* in north-east Spain. *Journal of applied Statistics* 29 (Special Issue): 125–142.

- Conroy MJ (2008) Some contributions of capture–recapture to evolutionary ecology and population modeling. In: Thomson DL, Cooch EG, Conroy MJ (eds.) *Modeling Demographic Processes in Marked Populations*. Environmental and Ecological Statistics, Springer, New York, Vol. 3, pp. 131–156.
- Cooch EG, Lank DB, Rockwell RF, Cooke F (1999) Body size and age of recruitment in snow geese *Anser c. caerulescens*. *Bird Study* (supplement) 46: 112–119.
- Cooch EG, Cam E, Link WA (2002) Occam's shadow: levels of analysis in evolutionary ecology – where to next? *Journal of Applied Statistics* 29 (Special Issue): 19–48.
- Cooch EG, White GW (2007) Using MARK – a gentle introduction. Available at <http://www.phidot.org/software/>
- Cormack RM (1964) Estimates of survival from the sighting of marked animals. *Biometrics* 51: 429–438.
- Coulson T, Benton TG, Lunberg P, Dall SRX, Kendall BE, Gaillard J–M (2006) Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proceedings of the Royal Society London B*: 273: 547–555.
- Crespin L, Harris MP, Lebreton J-D, Frederiksen M, Wanless S (2006) Recruitment to a seabird population depends on environmental factors and on population size. *Journal of Animal Ecology* 75: 228–238.
- Curio E (1983) Why do young birds reproduce less well? *Ibis* 125: 400–404.
- Danchin E, Boulinier T, Massot M (1998) Conspecific reproductive success and breeding habitat selection: implications for the evolution of coloniality. *Ecology* 79: 2415–2428.
- Danchin E, Heg D, Doligez B (2001) Public information and breeding habitat selection. In: Clobert J, Danchin E, Dhondt A, Nichols JD (eds), *Dispersal*, Oxford University Press, Oxford UK pp 243–258.
- Doligez B, Danchin E, Clobert J, Gustafsson L (1999) The use of conspecific reproductive success for breeding habitat selection in a non-colonial, hole-nesting species, the collared flycatcher. *Journal of Animal Ecology* 68: 1193–1206.
- Doligez B, Clobert J, Pettifor RA, Rowcliffe M, Gustafsson L, Perrins CM, McCleery RH (2002) Costs of reproduction: assessing responses to brood size manipulation on life-history and behavioural traits using multi-state capture-recapture models. *Journal of Applied Statistics* 29 (Special Issue): 407–423.
- Doligez B, Pärt T, Danchin E, Clobert J, Gustafsson L (2004) Availability and use of public information and conspecific density for settlement decisions in the collared flycatcher. *Journal of Animal Ecology* 73: 75–87.
- Doherty Jr. PF, Sorci G, Royle JA, Hines JE, Nichols JD, Boulinier T (2003) Sexual selection affects local extinction and turnover in bird communities. *Proceedings of the National Academy of Science U.S.A.*: 100: 5858–5862.
- Dugger BD, Blums P (2001) Effect of conspecific brood parasitism on host fitness for tufted duck and common pochard. *The Auk* 118: 717–726.
- Dupuis JA (1995) Bayesian estimation of movement and survival probabilities from capture–recapture data. *Biometrika* 82: 761–772.
- Dupuis JA (2002) Prior distributions for stratified capture–recapture models. *Journal of Applied Statistics* 29 (Special Issue): 225–237.
- Dupuis JA, Badia J, Maublanc M, Bon R (2002) Survival and spatial fidelity of moufflons (*Ovis gmelini*): a Bayesian analysis of age-dependant capture–recapture model. *Journal of Agricultural, Biological and Environmental Statistics* 7: 277–298.
- Emlen JM (1984) *Population biology – the coevolution of population dynamics and behaviour*. Macmillan, New York, U.S.A.
- Dupuis JA, Joachim J (2006) Bayesian estimation of species richness from quadrat sampling data in the presence of prior information. *Biometrics* 62: 706–712.
- Endler JA (1986) *Natural selection in the wild*. Princeton, University Press, Princeton, New Jersey, U.S.A.
- Ens JB, Weissing FJ, Drent R (1995) The despotic distribution and deferred maturity: two sides of the same coin. *The American Naturalist* 146: 625–650

- Fahrmeir L, Tutz G (1994) Multivariate statistics modelling based on generalized linear models. Springer-Verlag, New-York, Inc., New York.
- Fairbairn DJ, Reeve JP (2001) Natural Selection. In: Fox CW, Roff DA, Fairbairn DJ (eds) Evolutionary Ecology. Oxford University Press, Oxford, pp 29–43.
- Falconer DS, Mackay TFC (1996) Introduction to quantitative genetics, 4th edition, Longman, Harlow, U.K.
- Ferrière R, Dieckmann U, Couvet D (2004) Introduction. In: Ferrière R, Dieckmann U, Couvet D (eds) Evolutionary conservation biology. Cambridge University Press, Cambridge, pp 1–14.
- Festa-Bianchet M, Gaillard J-M, Jorgenson JT, Jullien J-M, Loison A (1999) Age-specific survival in five populations of ungulates: evidence of senescence. *Ecology* 80: 2539–2554.
- Fox CW, Roff DA, Fairbairn DA (2001) Preface. In: Fox CW, Roff DA, Fairbairn DJ (eds), Evolutionary Ecology, Oxford University Press, Oxford.
- Fox GA, Kendall BE (2002) Demographic stochasticity and the variance reduction effect. *Ecology* 83: 1928–1934.
- Fox GA, Kendall BE, Fitzpatrick JW, Woolfenden GE (2006) Consequences of heterogeneity in survival probability in a population of Florida scrub-jay. *Journal of Animal Ecology* 75: 921–927.
- Forslund P, Pärt T (1995) Age and reproduction in birds – hypotheses and tests. *Trends in Ecology and Evolution* 10: 374–378.
- Frankham R, Kingsolver J (2004) Responses to environmental change: adaptation or extinction. In: Ferrière R, Dieckmann U, Couvet D (eds) evolutionary conservation biology. Cambridge University Press, Cambridge, pp. 85–100.
- Freeman S, Herron JC (2000) Evolutionary analysis. Prentice Hall 2nd edition. Prentice Hall, Inc. Upper Saddle River, New Jersey, U.S.A.
- Frederiksen M, Bregnballe T (2001) Conspecific reproductive success affects age of recruitment in a great cormorant, *Phalacrocorax sinensis*, colony. *Proceedings of the Royal Society of London B*: 268: 1519–1526.
- Frétey T, Cam E, Le Garff B, Monnat J-Y (2004) Adult survival and temporary emigration in the common toad. *Canadian Journal of Zoology* 82: 859–872
- Fretwell SD, Lucas HL (1970) On territorial behaviour and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16–36.
- Fry JD (1992) The mixed-model analysis of variance applied to quantitative genetics: biological meaning of parameters. *Evolution* 46: 540–550.
- Futuyma DJ (1998) Evolutionary Biology. Sinauer, Sunderland, Massachusetts, U.S.A.
- Gaillard, J-M, Viallefont A, Loison A, Festa-Bianchet M (2004) Assessing senescence patterns in populations of large mammals. *Animal Biodiversity and Conservation* 27:47–58.
- Gilbert RO (1973) Approximation of the bias in the Jolly–Seber capture–recapture model. *Biometrics* 29: 501–526.
- Gimenez O, Covas R, Brown CR, Anderson MD, Brown MB, Lenormand T (2006) Nonparametric estimation of natural selection on a quantitative trait using mark-recapture data. *Evolution* 60: 460–466.
- Gregoire A, Preault M, Cezilly F, Wood MJ, Pradel R, Faivre B (2004) Stabilizing selection on the early expression of a secondary sexual trait in a passerine bird. *Journal of Evolutionary Biology* 17: 1152–1156.
- Green P (1995) Reversible jump Markoc chain Monte Carlo computation and Bayesian model determination. *Biometrika* 82: 711–732.
- Hadley GL, Rotella JJ, Garrott RA, Nichols JD (2006) Variation in probability of first reproduction of Weddell seals. *Journal of Animal Ecology* 75: 1058–1070.
- Hendry AP, Kinnison MT (1999) The pace of modern life: measuring rates of contemporary microevolution. *Evolution* 53: 1637–1653.
- Hernández-Lloreda MV, Colmenarez F, Arias RM (2003) Application of hierarchical linear modeling to the study of trajectories in behavioural development. *Animal Behaviour* 66: 607–613.

- Hestbeck JB, Nichols JD, Malecki RA (1991) Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. *Ecology* 72: 523–533.
- Hines JE (1994) MSSURVIV Users Manual. National Biological Service, Patuxent Wildlife Research Center, Laurel, MD 0708–4017. Available at: <http://www.mbr-pwrc.usgs.gov/software.html>
- Holt RD, Barfield M (2001) On the relationship between the ideal free distribution and the evolution of dispersal. In: Clobert J, Danchin E, Dhondt A, Nichols JD (eds), *Dispersal*. Oxford University Press, Oxford UK pp 83–95.
- Houle D (1991) Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. *Evolution* 45: 630–648.
- Houle D (1992) Comparing evolvability and variability of quantitative traits. *Genetics* 130: 195–204.
- Hougaard P (1991) Modeling heterogeneity in survival data. *Journal of Applied Probability* 28: 695–701.
- Ims RA, Hjermann DØ (2001) Condition-dependent dispersal. In: Clobert J, Danchin E, Dhondt A, Nichols JD (eds) *Dispersal*, Oxford University Press, Oxford UK pp 203–216.
- Jolly GM (1965) Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* 52: 225–247.
- Jolly GM (1993) Instinctive statistics. In: Lebreton J-D, North PM (eds) *Marked individuals in the study of bird populations*. Birkhäuser Verlag Basel, Switzerland, pp 1–5.
- Jones IL, Hunter FM, Robertson GJ, Fraser G (2002) Natural variation in the sexually selected feather ornaments of crested auklets (*Aethia cristatella*) does not predict future survival. *Behavioral Ecology* 15: 332–337.
- Kendall WL, Nichols JD (1995) On the use of secondary capture–recapture samples to estimate temporary emigration and breeding proportions. *Journal of Applied Statistics* 22: 751–762.
- Kendall BE, Fox GA (2001) Variation among individuals and reduced demographic stochasticity. *Conservation Biology* 16: 109–116.
- Kendall BE, Fox GA (2003) Unstructured individual variation and demographic stochasticity. *Conservation Biology* 17: 1170–1172.
- Kendall WL, Bjorkland R (2001) Using open robust design models to estimate temporary emigration from capture–recapture data. *Biometrics* 57: 1113–1122
- Kendall WL, Gould WR (2002) An appeal to undergraduate wildlife programs: send scientists to learn statistics. *Wildlife Society Bulletin* 30: 623–627.
- Kendall WL, Nichols LD (2002) Estimating state-transition probabilities for unobservable states using capture–recapture/resighting data. *Ecology* 83: 3276–3284.
- Kendall WL, Hines JE, Nichols JD (2003) Adjusting multi-state capture–recapture models for mis-classification bias: manatee breeding proportions. *Ecology* 84: 1058–1066.
- Kendall WL (2004) Copying with unobservable and mis-classified states in capture–recapture studies. Invited paper. *Animal Biodiversity and Conservation* 27: 97–107.
- Kendall WL, Nichols JD (2004) On the estimation of dispersal and movement of birds. *The Condor* 106: 720–731.
- Kéry M, Royle JA (2008) Inference about species richness and community structure using species-specific occupancy model in the national swiss breeding bird survey MHB. In: Thomson DL, Cooch EG, Conroy MJ (eds.) *Modeling Demographic Processes in Marked Populations*. Environmental and Ecological Statistics, Springer, New York, Vol. 3, pp. 639–656.
- King R, Brooks SP (2002) Bayesian model discrimination for multiple strata capture–recapture data. *Biometrika* 89: 785–806.
- King R, Brooks SP (2004) Bayesian analysis of the Hector’s dolphin data. *Animal Biodiversity and Conservation* 27: 343–354.
- Kinghorn B, Kinghorn S (2007) Pedigree. Available at <http://www.personal.une.edu.au/~bkinghor/pedigree.htm>
- Kingsolver JG, Smith SG (1995) Estimating selection on quantitative traits using capture–recapture data. *Evolution* 49: 384–388.

- Kruuk LEB, Clutton-Brock TH, Slate J, Pemberton JM, Brotherstone S, Guinness FE (2000) Heritability of fitness in a wild mammal population. *Proceedings of the National Academy of Sciences of the U.S.A.* 97: 698–703.
- Kruuk LEB, Merilä J, Sheldon BC (2001) Phenotypic selection on a heritable size trait revisited. *American Naturalist* 158: 557–571.
- Kruuk LEB (2004) Estimating genetic parameters in natural populations using the ‘animal model’. *Philosophical Transactions of the Royal Society London B.* 359: 873–890.
- Lande R, Arnold SJ (1983) The measurement of selection on correlated characters. *Evolution* 37: 1210–1226.
- Laurie WA, Brown D (1990) Population biology of marine iguanas (*Amblyrhynchus cristatus*) II. Changes in annual survival rates and the effects of size, sex, age and fecundity in a population crash. *Journal of Animal Ecology* 59: 529–544.
- Lebreton J-D, Clobert J (1986) User’s Manual for program SURGE, Montpellier, France: CEPE/CNRS.
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62: 67–118.
- Lebreton J-D, Hines JE, Pradel R, Nichols JD, Spendelov JA (2003) Estimation by capture–recapture of recruitment and dispersal over several sites. *Oikos* 101: 253–264.
- Liker A, Székely T (2005) Mortality costs of sexual selection and parental care in natural populations of birds. *Evolution* 59: 890–897.
- Levins R (1968) *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, U.S.A.
- Lindberg MS, Kendall WL, Hines JE, Anderson MG (2001) Combining band recovery data and Pollock’s robust design to model temporary and permanent emigration. *Biometrics* 57: 273–281.
- Link WA, Cooch EG, Cam E (2002a) Model-based estimation of individual fitness. *Journal of Applied Statistics* 29 (Special Issue): 207–224.
- Link WA, Cam E, Nichols JD (2002b) Of BUGS and birds. An introduction to Markov Chain Monte Carlo. *Journal of Wildlife Management* 66: 277–291.
- Link WA (2004) Individual heterogeneity and identifiability in capture–recapture models. *Animal Biodiversity and Conservation* 27: 87–91.
- Link WA, Barker RJ (2004) Hierarchical mark–recapture models: a framework for inference about demographic processes. *Animal Biodiversity and Conservation* 27: 441–449.
- Lukacs PL, Burnham KP (2005) Review of capture–recapture methods applicable to noninvasive genetic sampling. *Molecular Ecology* 14: 3909–3919.
- Lynch M, Walsh B (1998) *Genetics and analysis of quantitative traits*. Sinauer Associates Inc. Publishers, Sunderland, Massachusetts, U.S.A.
- MacKenzie DI, Kendall WK (2002) How should detection probability be incorporated into estimates of relative abundance? *Ecology* 83: 2387–2393.
- MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Lagtim CA (2002) Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83: 2248–2255.
- MacKenzie DI, Bailey LL (2004) Assessing the fit of site occupancy models. *Journal of Agricultural, Biological, and Environmental Statistics* 9: 300–318.
- MacKenzie DI, Bailey LL, Nichols JD (2004) Investigating species co–occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology* 73: 546–555.
- MacKenzie DI, Nichols JD (2004) Occupancy as a surrogate for abundance estimation. *Animal Biodiversity and Conservation* 27: 461–467.
- MacKenzie DI, Nichols JD, Royle AJ, Pollock KH, Bailey LL, Hines JE (2006) *Occupancy estimation and modeling. Inferring patterns and dynamics of species occurrence*. Academic Press, Elsevier Inc. Burlington, Massachusetts, U.S.A.
- Martin TE, Clobert J, Anderson DR (1995) Return rates in studies of life history evolution: are biases large? *Journal of Applied Statistics* 22: 863–875.

- Martin J, Nichols JD, Kitchens WM, Hines JE (2006) Multiscale patterns of movement in fragmented landscape and consequences on demography of the snail kite in Florida. *Journal of Animal Ecology* 75: 527–539.
- Massot M, Clobert J, Lecompte J, Barbault R (1994) Incumbent advantage in common lizards and their colonizing ability. *Journal of Animal Ecology* 63: 431–440.
- Massot M, Clobert J (2000) Processes at the origin of similarities in dispersal behaviour among siblings. *Journal of Evolutionary Biology* 13: 707–719.
- Matos CAP, Thomas DL, Gianola D, Tempelman RJ, Young LD (1997) Genetic analysis of discrete reproductive traits in sheep using linear and nonlinear models: I. Estimation of genetic parameters. *Journal of Animal Science* 75: 76–87.
- Mayr E (1997) This is biology: the science of the living world. The Belknap Press of Harvard University Press, Cambridge, Massachusetts, U.S.A.
- Mazer SJ, Damuth J (2001) Nature and causes of variation. Evolutionary significance of variation. In: Fox CW, Roff DA, Fairbairn DJ (eds) *Evolutionary Ecology*. Oxford University Press, Oxford, pp 3–28.
- McElligott AG, Altwegg R, Hayden TJ (2002) Age-specific survival and reproductive probabilities: evidence for senescence in male fallow deer (*Dama dama*). *Proceedings: Biological Sciences* 269 : 1129–1137.
- McGraw JB, Caswell H (1996) Estimation of individual fitness from life–history data. *American Naturalist* 147: 47–64.
- Mertz DB (1975) Senescent decline in flour beetle strains selected for early adult fitness. *Physiological Zoölogy* 48: 1–23.
- Metz JAJ, Nisbet RM, Geritz SAH (1992) How should we define ‘fitness’ for general ecological scenarios? *Trends in Ecology and Evolution* 7: 198–202.
- Mousseau TA, Fox CW (1998) The adaptive significance of maternal effects. *Trends in Ecology and Evolution* 13: 403–407.
- Nager RG, Monaghan P, Griffiths R, Houston DC, Dawson R (1999) Experimental demonstration that offspring sex ratio varies with maternal condition. *Proceedings of the National Academy of Science U. S. A.* 96: 570–573.
- Nichols JD, Pollock KH (1983) Estimating taxonomic diversity, extinction rates and speciation from fossil data using capture–recapture models. *Paleobiology* 9: 150–163.
- Nichols JD, Hines JE, Pollock KH, Hinz RL, Link WA (1994) Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. *Ecology* 75: 2052–2065.
- Nichols JD, Kendall WL (1995) The use of multi-state capture–recapture models to address questions in evolutionary ecology. *Journal of Applied Statistics* 22: 835–846.
- Nichols JD, Hines JE, Blums P (1997) Tests for senescent decline in annual survival probabilities of Common Pochards, *Aythya ferina*. *Ecology* 78: 1009–1018.
- Nichols JD, Boulinier T, Hines JE, Pollock KH, Sauer JR (1998a) Estimating rates of local extinction colonization and turnover in animal communities. *Ecological Applications* 8: 1213–1225.
- Nichols JD, Boulinier T, Hines JE, Pollock KH, Sauer JR (1998b) Inference methods for spatial variation in species richness and community composition when not all species are detected. *Conservation Biology* 12: 1390–1398.
- Nichols JD, Hines JE, Lebreton J-D, Pradel R (2000) The relative contribution of demographic components to population growth: a direct estimation approach based on reverse-time capture–recapture. *Ecology* 81: 3362–3376.
- Nichols JD (2002) Discussion comments on: “Occam’s shadow: levels of analysis in evolutionary ecology – where to next?” by Cooch, Cam and Link. *Journal of Applied Statistics* 29 (Special Issue): 49–52.
- Nichols JD, Kendall WL, Hines JE, Spendelov JA (2004) Estimation of sex-specific survival from capture–recapture data when sex is not always known. *Ecology* 85: 3192–3201.
- Norris JL, Pollock KH (1996) Nonparametric MLE under two closed capture–recapture models with heterogeneity. *Biometrics* 52:639–649.

- Oro D, Pradel R (2000) Determinant of local recruitment in a growing colony of Audouin's gull. *Journal of Animal Ecology* 69: 119–132.
- Orzack SH, Tuljapurkar S (2001) Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology* 82: 2659–2665.
- Otis DL, White GC (2004) Evaluation of ultrastructural and random effects band recovery models for estimating relationships between survival and harvest rates in exploited populations. *Animal Biodiversity and Conservation* 27: 157–173.
- Owens IPF, Bennett PM (1994) Mortality costs of parental care and sexual dimorphism in birds. *Proceedings of the Royal Society London B: Biological Sciences* 257: 1–8.
- Petit E, Valière N (2006) Estimating population size with non-invasive capture–recapture data. *Conservation Biology* 20: 1062–1073.
- Pettifor RE, Perrins CM, McCleery RH (1988) Individual optimization of clutch size in great tits. *Nature* 336: 160–162.
- Pettifor RE, Perrins CM, McCleery RH (2001) Individual optimization of fitness: variation in reproductive output, including clutch size, mean nestling mass and offspring recruitment, in manipulated broods of great tits *Parus major*. *Journal of Animal Ecology* 70: 62–79.
- Pigliucci M (2006) Genetic variance–covariance matrices: a critique of the evolutionary quantitative genetics research program. *Biology and Philosophy* 21: 1–23.
- Pledger S, Efford M (1998) Correction of bias due to heterogeneous capture probability in capture–recapture studies of open populations. *Biometrics* 54: \*898.
- Pledger S, Schwarz CJ (2002) Modelling heterogeneity of survival as a random effect using finite mixtures. *Journal of Applied Statistics* 29 (Special Issue): 315–327.
- Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107: 1–97.
- Pollock KP (2002) The use of auxiliary variables in capture–recapture modeling: an overview. *Journal of Applied Statistics* 29 (Special Issue): 85–102.
- Pradel R, Cooch EG, Cooke F (1995) Transient animals in a resident population of snow geese: local emigration or heterogeneity? *Journal of Applied Statistics* 22: 695–710.
- Pradel R (1996) Utilization of capture–mark–recapture for the study of recruitment and population growth rate. *Biometrics* 52: 703–709.
- Pradel R, Lebreton JD (1999) Comparison of different approaches to the study of local recruitment of breeders. *Bird Study* 46 (supplement): 74–81.
- Pradel R, Wintrebert CMA, Gimenez O (2003) A proposal for a goodness-of-fit test to the Arnason–Schwarz multisite capture–recapture model. *Biometrics* 59: 43–53.
- Promislow DEL, Montgomerie R, Martin TE (1992) Mortality costs of sexual dimorphism in birds. *Proceedings of the Royal Society London B: Biological Sciences* 250: 143–150.
- Quinn JL, Charmantier A, Garant D, Sheldon BC (2006) Data depth, data completeness and their influence on quantitative genetics estimation. *Journal of Evolutionary Biology* 19: 994–1002.
- Réale D, Festa-Bianchet M (2000) Quantitative genetics of life-history traits in a long-lived wild mammal. *Heredity* 85: 593–603.
- Réale D, Berteaux D, McAdam AG, Boutin S (2003) Lifetime selection on heritable life-history traits in a natural population of red squirrels. *Evolution* 57: 2416–2423.
- Reed ET, Gautier G, Giroux JF (2004) Effects of spring conditions on breeding propensity of greater snow goose females. *Animal Biodiversity and Conservation* 27: 35–46.
- Reed WL, Clark ME, Parker PG, Raouf SA, Arguedas N, Monk DS, Snajdr E, Nolan Jr V, Ketterson ED (2006) Physiological effects on demography: a long-term experimental study of testosterone's effects on fitness. *American Naturalist* 167: 667–683.
- Reekie EG, Budge S, Baltzer JL (2002) The shape of the trade-off function between reproduction and future performance in *Plantago major* and *Plantago rugelii*. *Canadian Journal of Botany* 80: 140–150.
- Rexstad E, Burnham KP (1991) User's guide for interactive program CAPTURE. Colorado Cooperative Fish and Wildlife Research Unit, Fort Collins, Colorado, U. S. A.

- Reznick D, Nunney L, Tessier A (2000) Big houses, big cars, superfleas and the cost of reproduction. *Trends in Ecology and Evolution* 15: 421–425.
- Reznick D, Rodd H, Nunnery L (2004) Empirical evidence for rapid evolution. In: Ferrière R, Dieckmann U, Couvet D (eds) *Evolutionary conservation biology*. Cambridge University Press, Cambridge, pp 101–118.
- Ricklefs RE (2000) Intrinsic aging-related mortality in birds. *Journal of Avian Biology* 31: 103–111.
- Ricklefs RE, Scheuerlein A (2001) Comparison of age-related mortality among birds and mammals. *Experimental Gerontology* 36: 845–857.
- Roff DA (1992) *The evolution of life histories*. Chapman and Hall, New York, U.S.A.
- Roff DA (2001) Age and size at maturity. In: Fox CW, Roff DA, Fairbairn DJ (eds), *Evolutionary Ecology*. Oxford University Press, Oxford, pp 99–112.
- Ronce O, Clobert J, Massot M (1998) Natal dispersal and senescence. *Proceedings of the National Academy of Science U. S. A.* 95: 600–605.
- Ronce O, Olivieri I, Clobert J, Danchin E (2001) Perspectives on the study of dispersal evolution. In: Clobert J, Danchin E, Dhondt A, Nichols JD (eds) *Dispersal*. Oxford University Press, Oxford UK pp 341–357.
- Royle JA, Link WA (2002) Random effects and shrinkage estimation in capture–recapture models. *Journal of Applied Statistics* 29 (Special Issue): 329–351.
- Royle JA, Nichols JD, Kéry M (2005) Modeling occurrence and abundance of species when detection is imperfect. *Oikos* 110: 353–359.
- Royle JA (2007) Modeling individual effects in the Cormack-Jolly-Seber model: a state-space formulation. *Biometrics* 63: 568–578.
- Royle JA (2008) Analysis of capture-recapture models with individual covariates using data augmentation. *Biometrics*. 2008 Apr 15. [Epub ahead of print].
- Royle JA, Kéry M (2007) Analysis of multinomial models with unknown index using data augmentation. *Journal of Computational and Graphical Statistics* 16: 67–85.
- Runge MC, Johnson FA (2002) The importance of functional form in optimal control solutions of problems in population dynamics. *Ecology* 83:1357–1371.
- Saccheri I, Hanski I (2006) Natural selection and population dynamics. *Trends in Ecology and Evolution* 21: 341–346.
- Saxton AM (2004) *Genetic analysis of complex traits using SAS*. SAS Institute Inc. Cary, North Carolina, U.S.A.
- Schaeffer LR (2004) Application of random regression models in animal breeding. *Livestock Production Science* 86: 35–45.
- Schmidt BR, Schaub M, Anholt BR (2002) Why you should use capture–recapture methods when estimating survival and breeding probabilities: on bias, temporary emigration, overdispersion and common toads. *Amphibia-Reptilia* 23: 375–388
- Schwarz CJ, Arnason AN (2000) Estimation of age-specific breeding probabilities from capture–recapture data. *Biometrics* 56: 59–61.
- Schwarz CJ, Stobo WT (2000) Estimation of juvenile survival, adult survival, and age-specific pupping probabilities for the female grey seal (*Halichoerus grypus*) on Sable Island from capture–recapture data. *Canadian Journal of Fisheries and Aquatic Sciences* 57: 247–253.
- Schwarz CJ, Arnason AN (2001) Comment on Schwarz and Arnason: estimation of age-specific breeding probabilities from capture–recapture data – authors reply. *Biometrics* 57: 976.
- Seber GAF (1965) A note on the multiple recapture census. *Biometrika* 52: 249–259.
- Seber GAF, Schwarz CJ (2002) Capture–recapture: before and after EURING 2000. *Journal of Applied Statistics* 29 (Special Issue): 5–18.
- Serrano D, Tella JL, Forero MG, Donazar JA (2001) Factors affecting breeding dispersal in the facultatively colonial lesser kestrel: individual experience vs. conspecific cues. *Journal of Animal Ecology* 70: 568–578.
- Serrano D, Tella JL (2003) Dispersal within a spatially structured population of lesser kestrels: the role of spatial isolation and conspecific attraction. *Journal of Animal Ecology* 72: 400–410.

- Serrano D, Oro D, Ursúa E, Tella JL (2005) Colony size selection determines adult survival and dispersal preferences: Allee effects in a colonial bird. *American Naturalist* 166: 22–31.
- Senar JC, Conroy MJ, Borras A (2002) Asymmetric exchange between populations differing in habitat quality: a metapopulation analysis of the Citril Finch. *Journal of Applied Statistics* 29 (Special Issue): 425–442.
- Service PM (2000) Heterogeneity in individual mortality risk and its importance for evolutionary studies of senescence. *The American Naturalist* 156: 1–13.
- Service PM (2004) Demographic heterogeneity explains age-specific patterns of genetic variance in mortality rates. *Experimental Gerontology* 39: 25–30.
- Sheldon BC, Kruuk LEB, Merilä J (2003) Natural selection and inheritance of breeding time and clutch size in collared flycatcher. *Evolution* 57: 406–420.
- Skalski JR, Hoffman A, Smith SG (1993) Testing the significance of individual- and cohort-level covariates in animal survival studies. In: Lebreton JD, North PM (eds) *Marked individuals in the study of bird population*. Birkhauser Verlag, Basel, Switzerland, pp 9–29.
- Skvarla JL, Nichols JD, Hines JE, Waser PM (2004) Modeling interpopulation dispersal by banner-tailed kangaroo rats. *Ecology* 85: 2737–2746.
- Stenseth NC, Saetre G-P (2003) Sexual selection forms the structure and dynamics of ecological communities. *Proceedings of the National Academy of Science U.S.A.* 100: 5576–5577.
- Smith SG, Skalski JM, Schlethe JW, Hoffman A, Cassen V (1994) SURPH. Statistical survival analysis of fish and wildlife tagging studies. Center for Quantitative Sciences, University of Washington, Seattle, Washington, U.S.A.
- Stearns SC (1992) *The evolution of life histories*. Oxford University Press, New York, U.S.A.
- Spiegelhalter DJ, Thomas A, Best NG, Gilks WR (1996) BUGS 1.4. Bayesian inference using Gibbs sampling Manual <http://www.mrc-bsu.cam.ac.uk/bugs/>.
- Spiegelhalter DJ, Best NG, Carlin BP, van der Linde A (2002) Bayesian measures of model complexity and fit. *Journal of the Royal Statistical Society, Series B.* 64: 583–639.
- Spendelov JA, Nichols JD, Nisbet ICT, Hays H, Cormons GD, Burger J, Safina C, Hines JE, Gochfeld M (1995) Estimating annual survival and movement rates of adults within a metapopulation of roseate terns. *Ecology* 76: 2415–2428.
- Spendelov JA, Nichols JD, Hines JE, Lebreton J-D, Pradel R (2002) Modelling postfledging survival and age-specific breeding probabilities in species with delayed maturity: a case study of Roseate terns at Falkner island, Connecticut. *Journal of Applied Statistics* 29 (Special Issue): 385–405.
- Tatar M (2001) Senescence. In: Fox CW, Roff DA, Fairbairn DJ (eds) *Evolutionary ecology*. Oxford University Press. Oxford, pp 128–141.
- Tinbergen JM, Sanz JJ (2002) Strong evidence for selection for larger brood size in a great tit population. *Behavioral Ecology* 15: 525–533.
- Tinbergen JM, Both C (1999) Is clutch size individually optimized? *Behavioral Ecology* 10: 504–509.
- Thomas SC, Coltman DW, Pemberton JM (2002) The use of marker-based relationship information to estimate the heritability of body weight in a natural population: a cautionary tale. *Journal of Evolutionary Biology* 15: 92–99.
- Török J, Hegvi G, Tóth L, Kőnczey R (2004) Unpredictable food supply modifies costs of reproduction and hampers individual optimization. *Oecologia* 141: 432–443.
- Tuomi J, Hakala T, Haukioja E (1983) Alternative concept of reproductive effort, costs of reproduction and selection in life-history evolution. *American Zoologist* 23: 25–34.
- Uller T, Massot M, Richard M, Lecompte J, Clobert J (2004) Long-lasting fitness consequences of prenatal sex-ratio in a viviparous lizard. *Evolution* 58: 2511–2516.
- Van de Pol M, Verhulst S (2006) Age-dependent traits: a new statistical model to separate within- and between-individual effects. *American Naturalist* 167: 766–773
- Van-Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life-history tactics. *The American Naturalist* 128: 137–142.

- Vaupel JW, Yashin AI (1985a) Heterogeneity's ruses: some surprising effects of selection on population dynamics. *The American Statistician* 39: 176–185.
- Vaupel JW, Yashin AI (1985b) The deviant dynamics of death in heterogeneous populations. In: Brandon Tuma N (ed) *Sociological methodology*. Jossey-Bass, Inc., Publishers. San Francisco, California, U.S.A. pp 180–211
- Viallefont A, Cooch EG, Cooke F (1995a) Estimation of trade-offs with capture–recapture models: a case study on the lesser snow goose. *Journal of Applied Statistics* 22: 847–861.
- Viallefont A, Cooke F, Lebreton J-D (1995b) Age-specific costs of first-time breeding. *Auk* 112: 67–76.
- Vounatsou P, Smith AFM (1995) Bayesian analysis of ring-recovery data via Markov Chain Monte Carlo simulation. *Biometrics* 51: 687–708.
- Webb JK (2006) Effects of tail autotomy on survival, growth and territory occupation in free-ranging juvenile geckos (*Oedura lesueurii*). *Austral Ecology* 31: 432–440.
- Weimerskirch H, Lallemand J, Martin J (2005) Population sex ratio in a monogamous long-lived bird, the wandering albatross. *Journal of Animal Ecology* 74: 285–291.
- White GC, Burnham KP, Otis DL, Anderson DR (1978) Users Manual for Program CAPTURE, Utah State Univ. Press, Logan, Utah. <http://www.mbr-pwrc.usgs.gov/software.html>
- White GC (1983) Numerical estimation of survival from recovery and biotelemetry data. *Journal of Wildlife Management* 47: 716–728.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (supplement): 120–138.
- White GC (2002) Discussion comments on: the use of auxiliary variables in capture–recapture modeling. An overview. *Journal of Applied Statistics* 29 (Special Issue) 103–106.
- Wiggins DA (1989) Heritability of body size in cross-fostered tree swallow broods. *Evolution* 43: 1808–1811.
- Wikelski M, Trillmich F (1997) Body size and sexual dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. *Evolution* 51: 922–936.
- Wilson AJ, Kruuk LEB, Coltman DW (2005) Ontogenetic patterns in heritable variation for body size: using random regression models in a wild ungulate population. *American Naturalist* 166: 177–192.
- Williams BK, Nichols JD, Conroy MJ (2002) Analysis and management of animal populations. Academic Press, San Diego, California, U.S.A.
- Wintrebert CMA, Zwinderman AH, Cam E, Pradel R, van Houwelingen JC (2004) Joint modelling of breeding and survival in the kittiwake using frailty models. *Ecological modelling* 181: 203–213.
- Williams GC (1992) Natural selection. Oxford University Press, Oxford.
- Williams PD, Day T, Fletcher Q, Rowe L (2006) The shaping of senescence in the wild. *Trends in Ecology and Evolution* 21: 458–463.
- Yashin AI, Iachine IA, Begun AZ, Vaupel JW (2001) Hidden frailty: myths and reality. Working paper. University of southern Denmark, Department of Statistics. ISBN 87-90700-41-4. Available at: <http://demografie.de>
- Yoccoz NG, Erikstad KE, Bustnes JO, Hanssen SA, Tveraa T (2002) Costs of reproduction in common eiders (*Somateria mollissima*): an assessment of relationships between reproduction effort and future survival and reproduction based on observational and experimental studies. *Journal of Applied Statistics* 29 (Special Issue): 57–64.