Demographic Concepts and Research Pertaining to the Study of Wild Primate Populations

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KEY WORDS   life cycle; population growth rate; behavioral ecology; life history; population genetics; conservation

ABSTRACT   Demography is the study of individuals as members of a population. The dynamics of a population are determined by collectively analyzing individual schedules of survival, growth, and reproduction. Together, these schedules are known as the vital rates of the population. The vital rates, along with dispersal, contribute to population structure, which refers to how the population is organized by age, sex, density, and social groups. I briefly review the history of anthropological demography as it pertains to wild primates and then I discuss basic demographic concepts and approaches for studying wild primate populations. I then turn to demographic studies of wild primate demography. Primates are generally characterized by high adult survival probabilities relative to survival at other age/stage classes and most primate populations have population growth rates near equilibrium. Changes in adult survival have the greatest impact on population growth rate (i.e., fitness) relative to other demographic traits such as juvenile/yearling survival or age at first reproduction. I discuss how these demographic patterns, and others, connect to topics and issues in behavioral ecology, life history theory, population genetics, and conservation biology. These connections help reaffirm the fact that the vital rates are both targets and agents of evolutionary change. In this regard, demographic studies of wild primates provide a critical link between the proximate socioecological processes that operate in a species and the long-term phylogenetic patterns that characterize a species. Yrbk Phys Anthropol 54:63–85, 2011.   © 2011 Wiley Periodicals, Inc.

INTRODUCTION TO PRIMATE DEMOGRAPHY

Demography is the study of individuals as members of a population. While traditionally conceived as the study of human populations, today the field of demography encompasses any study—human, plant, or animal—in which individual patterns of fertility, growth, recruitment, dispersal, and mortality are collectively analyzed for their population-level consequences. Demographic studies often focus on two interrelated topics, population structure and population dynamics. Population structure is defined by how the population is organized by sex and age classes, as well as the spatial organization of the population into social groups and other units. Population dynamics focuses on how important population-level parameters change over time; examples of these parameters include rates of fertility, dispersal, and mortality as well as the rate of population growth itself. Population structure is really a "snapshot" or "time-slice" of the population as it evolves and changes through time. The major goal of demography is to analyze a population in terms of its structure and to study the factors that determine its dynamics.

Demography has a long history, and perhaps the first formal paper to assemble information on births, deaths and their causes was by John Graunt, "Natural and Political Observations Mentioned in a Following Index, and Made Upon the Bills of Mortality," in 1661. Whipple (1919, cited in Skalski et al., 2005) noted the construction of a life table for a Polish village by Halley in 1692 and also gives other examples of life tables developed in the 19th century. Since then demographers have been studying human populations from just about every angle, and both cultural and biological anthropologists have contributed their own ideas to this growing body of theory (Kertzer, 2005). As noted by Johnson-Hanks (2007), anthropological demography has three main areas: 1) the merging of biological anthropology with population biology, behavioral ecology, and life history theory to study human groups (e.g., Hill and Hurtado, 1996); 2) the integration of (poststructuralist) studies of technology and political/economic power and the use of nonbiological explanations for explaining demographic trends (e.g., Rivkin-Fish, 2003); and, 3) the incorporation of "traditional" cultural and ethnographic topics such as kinship systems, marriage and inheritance patterns, and culturally specific patterns of fertility and migration, into demographic theory (e.g., Roth, 2004). Yet, formal demographic theory as applied to wild nonhuman primates is a relatively new phenomenon. That is, many of the early studies of wild primate populations did not emphasize the study of fertility, survival, and mortality rates as a stand-alone theoretical topic. This is likely because the unit of analysis in most primate field studies was,

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and remains, the social group. Explaining primate sociality in terms of the individual interactions, as well as the ecological and social forces maintaining group cohesion, formed the key paradigm for primate research throughout most of the 20th century (Sussman, 2011). This was aptly summed up by Trivers (1974) in a review of the book "The social behavior of monkeys," when he wrote, "...all questions of function are deferred to a final chapter that concerns itself only with why monkeys run around in groups (1974:163)." Many of the demographic studies published in the middle of the 20th century did not trickle into the primatological literature (e.g., Leopold, 1933; DeLury, 1947; Kelker, 1947; Severinghaus and Maguire, 1955; Davis, 1957), likely because these studies focused on wildlife management and not behavior (e.g., Hanson, 1963), and did not have much of an evolutionary thread. No doubt, many early primatological studies saw the value in studying patterns and causes of births and deaths (e.g., Schultz, 1961; Rowell, 1967). However, in these studies, the demographic properties of a population are mostly noted in the context of how they influence social behaviors and not vice versa. Primatologists—for the most part—were focused on the functional and evolutionary aspects of sociality and not demography per se.

What helped make demography an established component of primatology was the increasing recognition of a series of evolutionary-focused theoretical studies published between 1950 and 1970. These studies included the evolution of senescence, tackled independently by Medewar (1952), Hamilton (1966); and Williams (1957, 1966); the evolution of semelparity versus iteroparity (Cole, 1954); the evolution of r-K life history strategies (Lewontin, 1965), a theoretical exploration of life history evolution (Gadgil and Bossert, 1970), and an emphasis on the life cycle as a phenotype (Bonner, 1965). All of these authors sought to analyze aspects of life-cycle evolution, and in doing so, provided a foundation for evolutionary demography. Further, there was increasing emphasis on developing life tables for wild populations (Deevey, 1947; Quick, 1963). Demographic approaches to primate social behaviors began to emerge in the early 1970s; these studies sought connections between social behaviors, ecology, and demography and framed their interpretations in an evolutionary context (e.g., Dunbar and Dunbar, 1976; Altmann and Altmann, 1979; Dittus, 1979). At the same time, formal demographic analyses of both wild and free-ranging primates were also put forth (e.g., Dittus, 1975; Sade et al., 1976; Teleki et al., 1976), as well as comparative aspects of primate demography and social organization (Jorde and Spuhler, 1974).

Since the 1980s, studies of primate demography have increased almost every year. The fact that demographic studies were generally underemphasized in the development of primate field studies was probably due to two related factors: 1) when compared to most other mammals primates are highly encephalized and socially complex creatures, so it made sense for researchers to focus on this apparent and intriguing aspect of their phenotype; and 2) demographic studies often require population-level data to estimate things like fertility, survival, dispersal rates, and sex-ratio; given the emphasis on social behavior, many early field studies focused on one or a few social groups and did not gather population-wide data. But this is changing. Using the "PrimateLit" database—a database for published studies on nonhuman primates—I did a keyword search for "behavior" and "demography" in 5-year increments from 1940 until 2010. There were no demographic studies (at least as indexed by the key word demography) from 1940 to 1960 in this database; beginning in 1960 or so, demographic studies began to appear in the professional literature, and during the last 5 years, there have been 926 studies indexed as demography in this database. A crude demonstration of the growing significance of demography is shown in Figure 1, which plots the ratio of demography studies to behavior studies through time.

Demographic studies of wild primates are increasingly recognized as a necessary component in the study of life history evolution, population genetics, and social behavior (Dunbar, 1987; Strier, 2002; Strier et al., 2010; Leigh and Blomquist, 2011). This is because the unit of study in demography is the population, and it is also the unit of evolution (e.g., Wright, 1931). Because of this focus, demography has strong ties to evolutionary theory (Metcalf and Pavard, 2007). A population evolves due to the random (e.g., genetic drift) and nonrandom (natural selection) survival and reproduction of individuals within it. The continuing scrutiny of evolutionary forces acting on individuals ultimately shapes the pattern of survival, growth, dispersal, and reproduction in the population. That is, individuals within a species evolve a specific pattern of demographic traits. This pattern of demographic traits can be represented as a life cycle (Fig. 2). The life cycle comprises the important biological stages that individuals in a population move through from birth through death. Every individual has a probability of surviving, growing, reproducing, and dying; a life cycle graph summarizes these probabilities, which can then be studied for their demographic consequences. An important demographic parameter that can be estimated from the life cycle is population growth rate. This parameter provides an indication of whether the population is increasing in size or likely to go extinct. More to the point, this parameter measures fitness in natural populations (Charlesworth, 1994; Caswell, 2001), and the major phenotypic components of fitness—the things which selection scrutinizes—are demographic traits. Demography provides an interface between the proximate socioecological processes that operate in a species (e.g., how dispersal and survival influence social group composition) and the long-term phylogenetic patterns (e.g., why some species are characterized by late recruitment and long lives) that characterize a species or higher taxa.

In this study, I review the theory, methods, and research pertaining to wild primate demography. My intended audience is primate behavioral ecologists who seek to understand more about demographic techniques as they apply to wild primate populations. Experienced demographers will likely find my review of demographic theory rather sparse. Throughout, I emphasize studies of single populations over broad interspecific studies, as these have been reviewed elsewhere (Gage, 1998; Lee, 1999; Kappeler and Pererira, 2004). Also a topic that I do not cover is the methods and theory behind estimating abundance and density; assessing the number of individuals per unit area is a major component of demography, but I do not go into the estimation procedures. Several recent reviews as they apply to primates can be found in Hassel-Finnegan et al. (2008), Fashing and Cords (2000), and especially Buckland et al. (2010a,b).
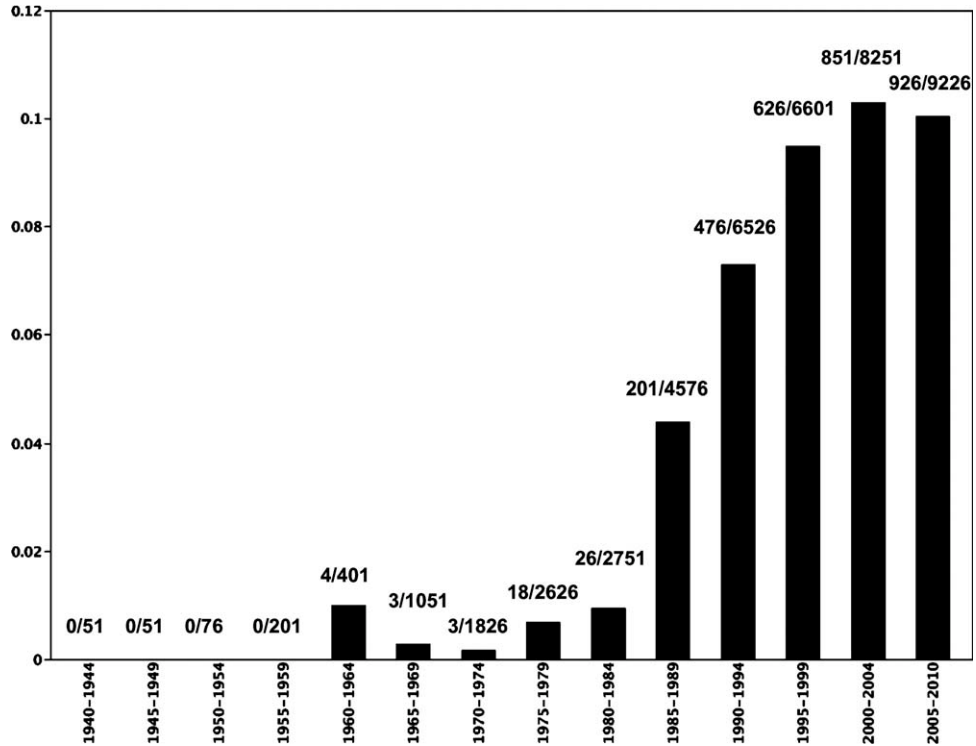
Fig. 1. The growth of demographic studies as indexed by "demography" and "behavior" in primatological research. The data represent the ratio of studies (demography/behavior) in 5-year increments and were compiled from the PrimateLit database.
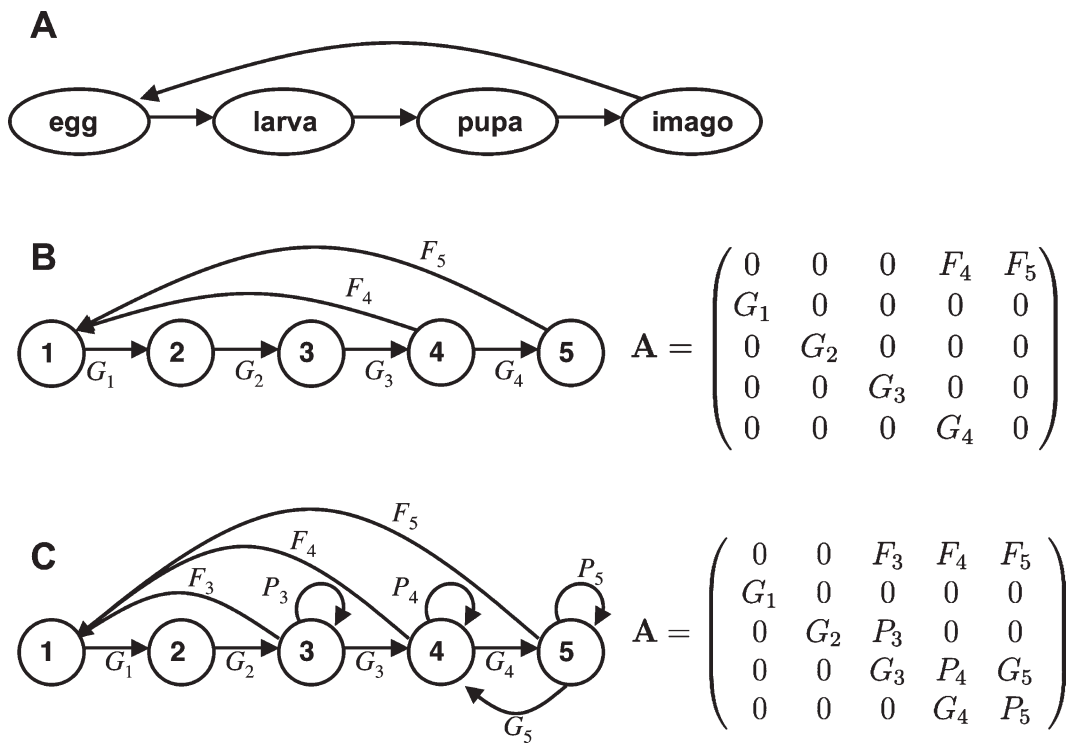
Fig. 2. Examples of life cycle graphs. An stage-based life cycle for insects is shown in **A**. A five-stage age-based life cycle is shown along with how the coefficients on the life cycle graph enter into a projection matrix is shown in **B**. An age- and stage-based life cycle graph and corresponding projection matrix is shown in **C**.

OVERVIEW OF DEMOGRAPHIC CONCEPTS

Demographic parameters

Populations structured by age or stage can be represented in a life cycle graph (Fig. 2). The life cycle graph embodies the biologically important stages of the organism. For a given species, there is no single "correct" life cycle graph; rather, these graphs are often developed using four interrelated criteria: 1) the ontogeny and ecology of the species under study; 2) a motivating demographic question; 3) the raw data that are available from the study species to "flesh out" or parameterize the life cycle graph; and 4) a general consideration of the life cycle in terms of complexity versus simplicity, for the purposes of estimating the parameters in the model (e.g., probabilities of survival, growth, etc.). For some species, it makes more sense to characterize their life cycle by stages rather than age. This is particularly relevant in plants and insects where there are biologically different phenotypes that characterize each life cycle stage. For example, some insects develop in four stages: egg, larva, pupa, and imago. This ontogenetic sequence conveniently implies a life cycle graph characterized by these four developmental stages (Fig. 2A). Primatologists tend to "think" in years. Thus, it is possible to develop a life cycle graph in which each stages corresponds to 1 year. Figure 2B shows a hypothetical organism that lives for 5 years and reproduces in its fourth and fifth years of life. It is possible to develop a life cycle graph combining both ages and stages, as shown in Figure 2C. In this life cycle, it is possible to "regress" into previous stages as well as to remain in the same stage over time. The arrows on the life cycle graph specify the direction of development and the "rules" for moving within and among stages over a given time period or projection interval. The projection interval can be any period of time (1 day, 1 week, 1 year, etc.) but usually a projection interval of 1 year is conventional. The life cycles also contain "fertility arrows," specifying reproduction from adult stages back to the first developmental stage. Life cycle graph construction deserves careful thought, and Caswell (2001), Yearsley and Fletcher (2002) and Cooch et al. (in press) provide more treatment of this topic.

The collective movement of animals through the life cycle is determined by the vital rates. The vital rates govern the changes in population size and composition over time and include fertility, survival, and growth. Operationally, many of the vital rates are expressed as probabilities of survival and transitions within the life cycle as well as number of offspring produced over the projection interval (these are represented as coefficients on the arrows in life cycle graphs shown in Fig. 2B,C). The vital rates can be used to calculate some important demographic parameters. One of the most important is the population growth rate or fitness, λ, which measures whether a population is growing or shrinking in absolute time. When $\lambda = 1$, the population is at equilibrium, when $\lambda > 1$ the population is growing and when $\lambda < 1$ the population is shrinking. λ is related to the intrinsic rate of increase, r, by $\lambda = e^r$, where e is the base of the natural logarithm (or $r = \ln \lambda$). Because the vital rates determine changes in population size based on individual risks of surviving, reproducing, and dying, it is possible to estimate λ from the overall number (N) of animals in the population across successive time points (t) or projection intervals,

$$\lambda = N_{t+1}/N_t \qquad (1)$$

Equation 1 also hints at the possibility of projecting future population size given the population growth rate. Population projection is a fundamental component of almost all demographic analyses. To determine the number of individuals in a population at t time points in the future (N_t) given an initial population size of N_0, the projection equation is

$$N_t = \lambda^t N_0 \qquad (2)$$

As will be discussed below, it is also possible to project a population using the vital rates rather than the number of animals in a population. When the vital rates remain constant, the proportion of animals in different age or stage classes will eventually remain the same across projection intervals; when this occurs, the distribution of individuals is known as the stable age (or stage) distribution. Reproductive value is another important demographic parameter that can be estimated from the vital rates. Reproductive value is the relative contribution of an individual in a particular age or stage to future population growth (Fisher, 1930). Another measure of fitness, particularly common in behavioral ecology, is net reproductive rate, R_0, which is the expected number of same-sexed offspring produced by an individual during their lifetime. Generation time is another parameter of interest to behavioral ecologists and it is also used in many population genetic models (e.g., Beaumont, 1999). There are several ways to define and calculate generation time, T, (Caswell, 2001); one method is to follow a group of animals from their birth and count up all their offspring they produced at ages x, taking the average of x provides a measure of generation time—the average age of reproduction. This method gives similar results to another measure of generation time—the time it takes for a population to grow by a factor R_0. In this latter case, $T = \ln (R_0)/\ln (\lambda)$.

Sensitivity analysis

Because of physiological, genetic, or functional constraints some vital rates are expected to vary more than others. Similarly, some vital rates might be positively or negatively correlated with other vital rates. And some vital rates—if perturbed or changed—might have a larger impact on population growth rate than other vital rates. Sensitivity analysis determines how a dependent variable will change (usually, in evolutionary demography, this variable is fitness, λ) given a change in one or more of the vital rates (or other independent variables). Sensitivity, s, is the partial derivative of λ with respect to some vital rate, θ, holding all other elements constant,

$$s(\theta) = \partial\lambda/\partial\theta \qquad (3)$$

Sensitivities have an interpretation as selection gradients (Lande, 1982; Barfield et al., 2011) since they measure the dependency of fitness on a particular life history trait. Essentially, $\partial\lambda/\partial\theta$ measures directional selection (i.e., the mean change) on the vital rate θ when all other vital rates are held constant. To measure changes in the variance in θ, it is necessary to calculate the second derivative of λ to θ or $\partial^2\lambda/\partial^2\theta$ (analogous to stabilizing/disruptive selection). While sensitivities

measure the effect of an absolute change in a vital rate, elasticities measure the effects of a proportional change. The elasticity, e, of a vital rate, θ, is

$$e(\theta) = \partial\lambda/\partial a_{ij} * \theta/\lambda$$
$$= \partial \log \lambda/\partial \log \theta \qquad (4)$$

Because elasticities measure proportional changes (or % changes), they sum to one. This makes it easier to compare changes in vital rates. For example, how does a 5% decrease in survival compare with a 5% decrease in fertility? Correlations among vital rates can also be accommodated using sensitivities and elasticities (van Tienderen, 1995; Caswell, 2001).

Environmental and demographic stochasticity

When environmental events are not predictable or recurrent they are referred to as stochastic. Incorporating environmental stochasticity into demographic analyses is straightforward. First, it is necessary to produce a model of stochastic environmental variation. Environmental models statistically capture states of the environment, where each environmental state refers to some factor that is thought to influence the vital rates of the population (e.g., rainfall). Examples of environmental states can be "high rainfall" and "low rainfall," or "abundant food," "average food," and "scarce food," or they can be continuous variables such as temperature or humidity. The states of the environment can be empirically derived, for example, using a historical sequence of annual rainfall amounts to develop a statistical sequence of environmental states, or the states can come from a parametric distribution of hypothetical environmental states that are thought to influence the vital rates. A mathematical function is used to link the model of environmental variation to the vital rates. When the vital rates have been linked to the environmental states, it is possible to project the population into the future to calculate the stochastic growth rate, λ_s, which reflects the rate of increase (or decrease) of the population in unpredictable environments. Numerous demographic parameters can be determined from stochastic environment models including the stage distribution, reproductive value, and sensitivity values (Tuljapurkar, 1990; Caswell, 2001; Lande et al., 2003).

Demographic stochasticity takes into account the randomness of individual survival and reproduction when populations are small. As discussed above, the vital rates provide the average probabilities of survival and transitions within and among stages in the life cycle. The average probability makes sense when we consider a large population of animals moving within and between stages; if the survival probability is 0.7 for a given stage, then 70% of the animals in that stage will survive. However, average probabilities do not necessarily apply to individual animals. An individual will or will not survive in a given stage and thus an individual cannot properly survive a given stage with a probability of 0.7. To account for this, it is necessary to treat the vital rates as random variables not as fixed quantities. Operationally, this entails that the value of each vital rate is drawn from a distribution or random number generator at each time step, and the animal's fate (survival or death) is associated with a particular value from the distribution or random number generator. The randomness of individual survival and growth influences the population's dynamics. In the same sense that a beneficial allele might be lost due to genetic drift in a small population; a small population with a positive population growth rate ($\lambda = 1.02$) might still decline to extinction because at each time step more individuals died than survived.

Mark-recapture estimation

A powerful method for estimating the vital rates is known as mark-recapture analysis. Mark-recapture methods take into account uncertainty when estimating abundance or other vital rates from marked animals. The earliest methods were premised on capturing, marking, and releasing a sample of animals at time t, then later recapturing a sample of animals at time $t + 1$. The recaptured sample will often contain a subset of the previously marked animals, and it is possible to estimate both the abundance of animals as well as the recapture probability from these data. These methods have been extended to the vital rates, not just abundance (e.g., Nichols, 1992; Fujiwara and Caswell, 2002). As an example, consider a marked adult female (call her female #45) in a species characterized by a birth season and a short period of offspring dependence. Females in this population are designated by the states "R" (with offspring) or "N" (without offspring). Each year the population is censused during the birth season and the reproductive status, R or N, is noted for each individually marked animal. No doubt, during some census years, some individual females will not be seen during the census period. This is designated as "0." Across 7 years, assume the recorded census history of female #45 is

R R N 0 0 N R

This census history for female #45 poses a problem with respect to estimating the vital rates. What was the reproductive state of #45 during the years when she was not seen? One possible census history for #45 over this time period is R R N **N N** N R (bolded values reflect assumed reproductive state); another possible census history is R R N **R R** N R; another is R R N **R N** N R; and so on. To account for this uncertainty, one can define a "recapture" probability, $p_{(i)}t$, which is the probability that an animal was recaptured (or just resighted/recensused) at time t in stage i. It is possible to write out each possible census history of each animal in terms of the recapture probability and vital rates (these are the model parameters). The parameters for each census history can be estimated using maximum likelihood to provide the best unbiased estimate of parameter values when taking into account missing animals. The literature on mark-recapture techniques is vast and highly statistical. A good introduction is found in Conroy and Carroll (2009); more technical treatments are given in Williams et al. (2002), and Amstrup et al. (2005).

BASIC DEMOGRAPHIC METHODS
Life table analysis

Many reviews of primate demography are based on the analysis of life tables so only a brief description will be provided here (see Richard, 1985; Dunbar, 1988). A life table is a representation of age-specific survivorship and reproduction. Most introductory treatments of life table analysis focus on the survival function, $l(i)$, which

is the probability of survival from birth to age i. Another important function is the mortality rate, $u(i)$, which is the rate at which individuals die over a short interval at age i (this is also known as the hazard function). The distribution of the age at death, $f(i)$, is the probability density function for the age at death. The reproductive (or maternity) function, $m(i)$, is defined as the number of offspring per individual of age i per unit time. From the life table functions, it is possible to calculate numerous demographic statistics such as reproductive value, stable age distribution, life expectancy, population growth rate, etc. (Caughley, 1977).

Matrix population models

Matrix population models (MPMs) are increasingly used to analyze wild primate populations (e.g., Alberts and Altmann, 2003; Lawler et al., 2009; Morris et al., 2011). MPMs are particularly heuristic because they are based on an age or stage-based projection matrix (Fig. 2). The life cycle graph is isomorphic with the projection matrix—a matrix that contains the vital rates (these are the coefficients in the life cycle graph in Fig. 2B,C). A n-stage life cycle graph has a $n \times n$ projection matrix. Age-based projection matrices are also known as "Leslie matrices" whereas stage-based projection matrices are known as Lefkovich matrices (Caswell, 2001). Figure 2B,C shows projection matrices, $\mathbf{A}$, developed from the corresponding life cycle graphs (the entries in $\mathbf{A}$ are indexed by the ith row and jth column, a_{ij}). Because the projection matrices contain vital rates and the vital rates determine population growth, it is possible to construct a population projection using the projection matrix. Using the notation of matrix algebra, define a vector of animals in each stage ($\mathbf{n}$) at time t. The projection matrix $\mathbf{A}$ is multiplied by this vector to determine the numbers of animals in stages next year, $\mathbf{n}(t + 1)$

$$\mathbf{n}(t + 1) = \mathbf{A}\mathbf{n}(t) \tag{5}$$

Essentially, animals in different stages in year t are multiplied by the probability of surviving, reproducing, and growing (i.e., making transitions in the life cycle as embodied in $\mathbf{A}$) to determine the animals in the stages in year $t + 1$. The output—next year's animals in each stage, $t + 1$—can then be "remultiplied" by $\mathbf{A}$ to get the following year's output, $t + 2$, and this process can be repeated numerous times. Numerous demographic parameters can be estimated from the projection matrix (Caswell, 2001).

Survival analysis

A different class of estimation procedures for estimating survival, mortality, or reproductive events uses survival analysis. These models are used when individuals are followed over time and their fate is recorded. Their fate might be death, giving birth to an offspring, or emigrating, and these models can accommodate censored data, as when the study has ended before tracking the ultimate biological fate of the animal. The data used to parameterize these models can come from life tables or from any source in which the animal's fate is recorded. There are parametric and nonparametric methods for estimating survival (or other events such as reproduction). Parametric models draw from a specific family of curves to model survival, mortality, or reproduction.

Nonparametric methods let the data determine the shape of the curve. Some of the most widely used parametric distributions are the Weibull, Gompertz, logistic, and Siler (Siler, 1979; Bronikowski et al., 2001; Skalski et al., 2005). All of these models can be used to generate age-specific survival curves (the probability of surviving from age i to age $i + 1$) as well as hazard functions (the rate at which an event will occur given survival to age i). The Siler model is particularly useful for modeling survival and mortality in primate and human populations (Gage and Dyke, 1986; Gage, 1988). This model has wide appeal and applicability because it breaks down survivorship into three phases, each with a corresponding survival function: juvenile, $l_j(i)$; adult, $l_a(i)$; and senescence, $l_s(i)$. The juvenile component uses the Gompertz function

$$l_j(i) = \exp[-a_1/b_1(1 - \exp[-b_1 i])] \tag{6}$$

where a_1 and b_1 are the parameters governing the shape of the survival curve during juvenility. The adult component has an exponential (exp) component

$$l_a(i) = \exp[-a_2 i] \tag{7}$$

where a_2 is the parameter describing the shape of the survival curve during adulthood. The senescent component also uses a Gompertz function

$$l_s(i) = \exp[-a_3/b_3(1 - \exp[-b_3 i])] \tag{8}$$

where a_3 and b_3 are the parameters dictating the shape of the survival curve during the senescent phase. The parameters in this model are analyzed concurrently to produce a particular hazard function and age-specific survivorship curve. The Siler model produces a hump-shaped age-specific survival curve, with low early survival, higher adult survival, and then low late survival (the hazard function is basically the opposite of the age-specific survival curve).

Nonparametric survival analyses include the Kaplan–Meier survival model and Cox proportional hazards. The Kaplan–Meier model estimates survival by keeping track of the numbers of individuals in three groups: an "at risk" group, r; a dead group, d; and a censored group, c. At each time step, the model estimates the cumulative survival (or hazard) of surviving to specific points in time. The general model for surviving over the interval t to $t + 1$, conditional on surviving to time t is

$$S(t) = (r_t - d_t)/r_t \tag{9}$$

where r_t is the number of animals alive but that are at risk of death over the interval t to $t + 1$, and d_t is the number of animals that died over the interval t to $t + 1$. Censored animals are taken into account by recalculating the r_t values at each time step and eliminating censored animals. Survival analyses generate a survival curve (usually a stepped curve) that provides information on the probability that an individual will be alive past time t. The Cox proportional hazards model constitute another nonparametric model for estimating survival or other events such as reproduction. The general model takes the form of a hazard function, in which an individual experiences a hazard (e.g., death or giving

birth) at time t, given a set of explanatory variables (e.g., predation rate or food supply), $\mathbf{x}$, in vector form

$$h(t, \mathbf{x}) = h_0(t) \exp \Sigma \beta_i x_i \qquad (10)$$

where $h_0(t)$ represents the baseline hazard, and the exponential (exp) is the linear sum of explanatory variables, x_i, multiplied by the parameters, β_i (the summation is over the number of explanatory variables). Cox proportional hazard models are popular because they often approximate parametric models but do not make a priori assumptions about the shape of the hazard function.

Other "question-specific" models in demography

The above models might be considered formal demographic models because they are based on a well-characterized and generalizable theoretical framework. Other demographic models are constructed based on a particular question. These models can be deterministic, in which the model output is a "fixed" function of model input and assumptions, or the models can be probabilistic in which each run of the model produces a different output because some variables are drawn from a probability distribution. One increasingly popular type of probabilistic model is an individual-based model (IBM). IBMs are only beginning to be applied in primate demography (e.g., Wiederholt et al., 2010). IBMs are a powerful way to model social interactions and their influence on population-level dynamics in a spatially explicit setting (Grimm and Railsback, 2005). Within the model, each individual (or agent) is modeled explicitly along with its properties such as genotype, age, location, and different propensities for behavioral events (e.g., dispersal, aggression) given their location and other factors such as density. The model is then "run" and individuals are allowed to interact, disperse, die, reproduce, and the fitness consequences of each individual action are tabulated and analyzed.

CONCEPTUAL CONNECTIONS BETWEEN DEMOGRAPHY AND OTHER FIELDS

Table 1 summarizes some recent demographic studies that contain data on population growth rate, vital rates, sensitivity, and other demographic parameters. This table is not meant to be exhaustive, notably many of the important demographic studies conducted in the 1970s and 1980s are omitted because these studies are summarized elsewhere (Jolly, 1985; Richard, 1985; Dunbar, 1987; Dunbar, 1988). There are some interesting patterns in the data presented in Table 1. For example, across many species adult survival probabilities are larger than juvenile and infant survival probabilities. Further, many species have population growth rates that are near equilibrium (i.e., 0.98–1.03), and in cases where growth rates are different from equilibrium, more populations are marked by positive growth rates than negative ones ($\lambda > 1$). Similarly, for those studies that conducted sensitivity/elasticity analyses, λ is most sensitive to perturbations in adult survival. However, these data are better analyzed in terms of how they tie into other areas within primatology. I discuss the conceptual connections between demography and behavioral ecology, life history theory, population genetics, and conservation biology below. For each section, I try to make a conceptual point and/or I discuss "case-studies" that illustrate the different types of demographic methods and concepts described above.

Behavioral ecology and demography

Many behaviors are thought to have evolved to maximize one or more of the vital rates or some other important component of fitness (including inclusive fitness) (Danchin et al., 2008). In this regard, the connections between demography and behavioral ecology are numerous. One way to organize the connections between behavioral ecology and demography is to take a "selectionist" view of the life cycle. In moving from zygote to adult, there is selection on survival ability (viability selection); in attempting to find a mate as an adult, there is selection on mate acquisition (sexual selection); and once a mate or mates have been acquired, there is selection on the mating pair to produce viable and high-quality offspring (fertility selection) (Fig. 3). These are not the only types of selection that can act on the life cycle but these types of selection are discussed below to show the myriad ways in which demography and behavioral ecology intersect.

Viability selection and gregariousness. Viability selection occurs when there are differences among individuals in terms of survival. Numerous behavioral strategies are under the continuing scrutiny of viability selection including feeding strategies, predator avoidance, and gregariousness. Here, I focus on gregariousness. The division of a population into social groups is a major demographic feature of population structure that characterizes numerous primate species. Group living is expected to evolve when individual fitness is enhanced by associating with conspecifics (Krause and Ruxton, 2002). There have been numerous models that look at the formation of social groups, the benefits groups provide, and the processes through which groups survive over time, split, and dissolve. Sibly (1983) developed a simple model of group formation in which the fitness function relating individual fitness to group size was humped shaped with a long right tail. Sibly argued that if optimal group size was, say, 15 individuals (the fitness function peaks at 15), then optimal groups size is not stable and groups will be larger than optimal. The idea is that if a group is at its optimal size, 15, it will always be better for an additional individual to join the group of 15 rather than forage alone because the fitness function is higher at 16 than at 1. The same idea will apply to other "joiners;" they can either remain solitary or join the group. Only when the group gets to about 40 individuals does it pay to forage alone, since the fitness function is low but equal at 1 and 40 (Fig. 3).

Sibly's model provides a powerful "null" model of optimal group size based solely on the assumption that group-living enhances individual fitness. However, decades of field research on wild primates reveal that numerous ecological and social variables interact to determine group size and structure. In turn, the formation of social groups can shape patterns of selection on the vital rates, including survival and lifespan. Necessarily, models of sociality must include more realistic factors that capture the ecology of group formation. In this regard, it pays to examine a recent "question-specific" deterministic demographic model derived by Janson (2003). Janson (2003) considered the ecological and demographic factors influencing group size. Janson was motivated to assemble a demographic model of primate grouping patterns due to

TABLE 1. *Qualitative and quantitative description of population dynamics in wild primate populations*

Species	Survival/Mortality	Fertility	r or λ	Other statistics	Analysis	References
Propithecus verreauxi	$S_n = 0.527$ $S_j = 0.930$ $S_a = 0.927$	$F_j = 0.026$ $F_a = 0.164$	$\lambda = 0.98$	$T = 19.5$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Lawler et al. 2009; Morris et al. 2011
Cebus capucinus	$S_n = 0.793$ $S_j = 0.921$ $S_a = 0.965$	$F_j = 0.02$ $F_a = 0.145$	$\lambda = 1.02$	$T = 35.2$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Morris et al. 2011
Cercopithecus mitis	$S_n = 0.809$ $S_j = 0.961$ $S_a = 0.942$	$F_j = 0.049$ $F_a = 0.206$	$\lambda = 1.04$	$T = 25.1$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Morris et al., 2011
Brachyteles hypoxanthus	$S_n = 0.941$ $S_j = 0.954$ $S_a = 0.984$	$F_j = 0.040$ $F_a = 0.170$	$\lambda = 1.05$	$T = 70.1$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Morris et al. 2011
Papio cynocephalus	$S_n = 0.875$ $S_j = 0.920$ $S_a = 0.955$	$F_j = 0.057$ $F_a = 0.287$	$\lambda = 1.06$	$T = 28.1$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Morris et al. 2011
Pan troglodytes schweinfurthii	$S_n = 0.828$ $S_j = 0.956$ $S_a = 0.945$	$F_j = 0.021$ $F_a = 0.067$	$\lambda = 0.98$	$T = 34.0$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Morris et al. 2011
Gorilla beringei (Karisoke)	$S_n = 0.830$ $S_j = 0.972$ $S_a = 0.977$	$F_j = 0.020$ $F_a = 0.103$	$\lambda = 1.03$	$T = 52.9$ yrs Sensitivity of λ to adult survival is highest	Stage-based MPM	Morris et al., 2011
Propithecus diadema edwardsi	$S_n = 0.87$ $S_j = 0.67$ $S_a = 0.95$	Fecundity = 0.250	$\lambda = 0.99$	Sensitivity of λ to adult survival is highest	Stage-based MPM	Dunham et al., 2008
Alouatta palliata	$S_n = 0.67$		$\lambda = 1.09$	Ratio of immature to adult female = 0.9	Observational data	Arroyo-Rodriguez et al., 2008
Lemur catta	50% of newborn females survive to adulthood	Fecundity average = 0.66 for females aged 2–9	$\lambda = 1.03$		Observational data	Koyama et al., 2001 Koyama et al., 2002
Presbytis thomasi	Yearly survival rate, $p(x)$, is highest in adult animals	Average age-specific birth rate = 0.44	$\lambda = 1.01$	They document increasing population density over time	Age-based MPM	Wich et al., 2007
Alouatta seniculus	$S_n = 0.92$ $S_j = 0.87$ $S_{sa} = 0.81$ $S_a = 0.90$	Reproduction with surviving infant = 0.35	$\lambda = 0.65$ to 1.10 over 30 years	λ is most sensitive to adult female survival and reproduction	Census data and an individual based model	Rudran and Fernandez-Duque, 2003; Wiederholt et al., 2010
Pongo spp.	High yearly survival rates across all ages	18.2% of females breed when population density is low 11.1% of females breed when population density is at carrying capacity	$r_{max} = 0.02$ but negative realized growth rates	Hunting and habitat quality produce negative population growth rates; at current logging rates, population size is projected to decline to 0 in about 150 years	Census data, life table analysis, and a PVA	Marshall et al., 2010 Wich et al., 2004

λ or r refers to annual growth rate. Survival (*S*) and fertility (*F*) are subscripted by age class: newborn (n), juvenile (j), subadult (sa), and adult (a). *T* refers to generation time.
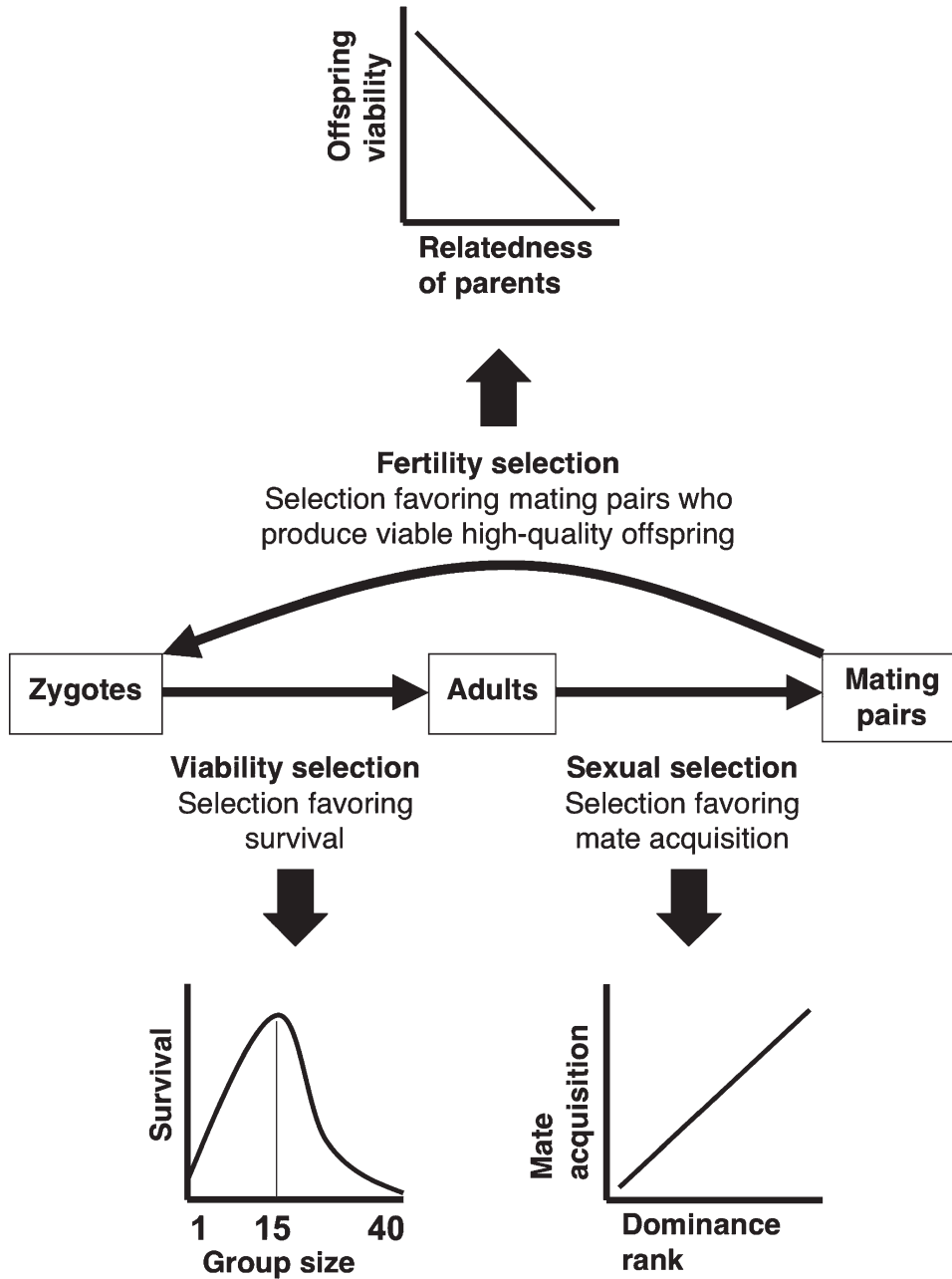
Fig. 3. Examples of the types of selection that act on individuals over their life cycle. Viability selection operates on individuals with respect to group formation. The key question in the evolution of group living is determining the shape and variables contributing to the fitness function that relates individual fitness to group size. Sexual selection results from variation in mate acquisition as when a dominant male usurps a subordinate's mates. Fertility selection results from variation in the production of offspring by mating pairs. Fertility selection likely underlies the evolution of sex-biased dispersal and philopatry.

three "puzzles" that characterize primate sociality as a response to predation. First, across species, there is a negative association between body size and predation rates (rate is defined as the number of individuals killed over time), despite the fact that increased body size is viewed as an adaptive response to predation risk (risk is the probability of death per individual); second, group size itself is negatively correlated with predation rates even though increased group size is also thought to be an adaptation against predation; and finally, if increased group size is an adaptation to lower predation, then in

predator-"reduced" environments there should be smaller group sizes, yet this pattern does not hold for the majority of primate species. Given these puzzles, Janson built a model of primate sociality in which fitness was a function of several important demographic and ecological parameters. An important parameter in the model, designated as C, measured the trade-off between foraging and predation risk. The demographic traits included fecundity, mortality, and juvenile age at maturity (and body size), while ecological parameters included resource abundance and predation rate. Janson
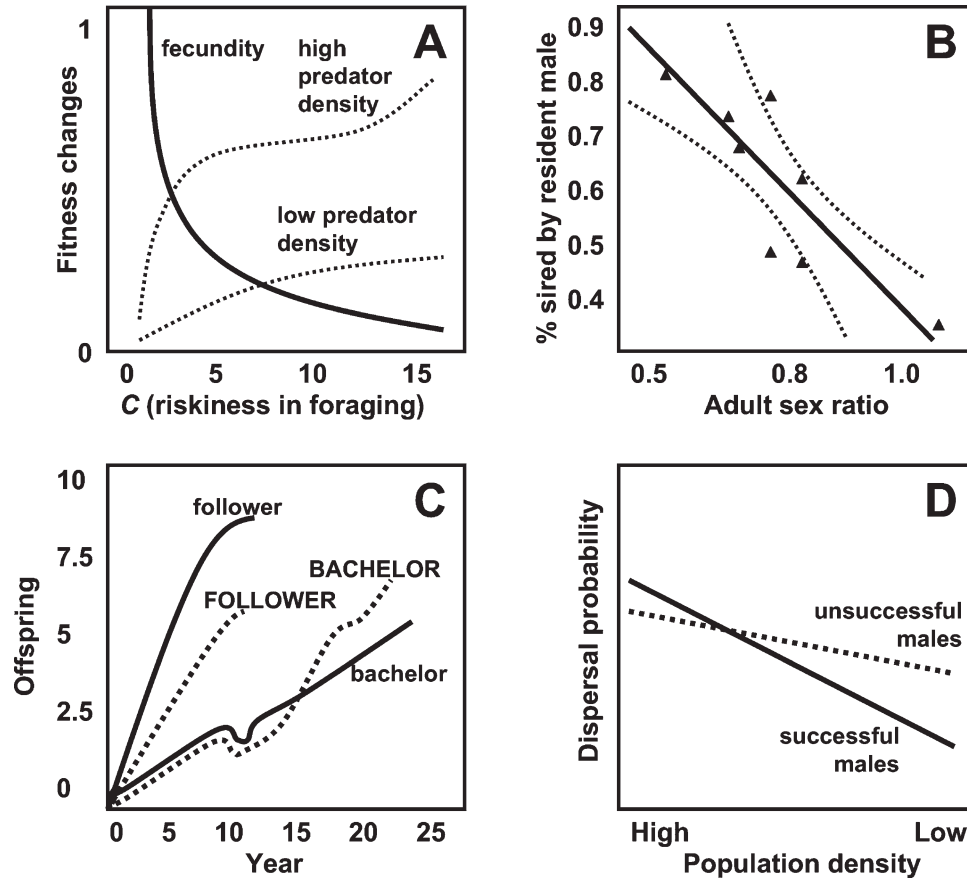
Fig. 4. Examples of demographic and ecological variables and their influence on fitness or dispersal. The relationship between fitness and risk-sensitive foraging (C) is shown in **A**; C is maximized at the intersection of predator density and fecundity. The relationship between percentage of offspring sired by resident males in their own group and the adult socionomic sex ratio of their group is shown in **B**; resident male sifaka cannot monopolize all fertilizations as the number of females in his group increases. The number of "offspring equivalents" expected to accumulate for "follower" and "bachelor" male gorillas over time is shown in **C**; followers accumulate more fitness in a shorter time, and the capital letters refer to different parameterizations of this model. The relationship between population density and dispersal probability for successful and unsuccessful male baboons is shown in **D**. A is redrawn from Janson (2003); B is redrawn from Lawler et al. (2003); C is redrawn from Watts (2000); and D is redrawn from Alberts and Altmann (1995). See text for further discussion.

analytically solved for the optimal value of C that maximizes fitness—the optimal level of risk-sensitive foraging where increased fecundity is balanced by increased mortality due to predation (Fig. 4A). In exploring the consequences of his model, Janson hit on the key demographic factor that helps solve the puzzles listed above. This factor is longevity. Long lifespans are associated with large body size and a long-lived creature has more to lose than a short-lived creature in terms of the fitness losses incurred by dying via predation. Thus, larger bodied primates should be selected to increase their antipredator adaptations to reduce the risk of predation. Increased sociality is one of these adaptations. This can explain why predation rates are reduced in large bodied, gregarious species—gregariousness reduces predation risk (as does larger-body size). Janson's model represents a unique approach to understanding a major determinant of primate social systems—predation—and he approaches the "predation problem" using demographic and life history variables. As shown in Table 1, adult survival is a major determinant of fitness in primate populations, so Janson's model is congruent with demographic analyses that were generated independent of the issue of predation.

Sexual selection and mating strategies. Sexual selection occurs when there is variation with respect to mate acquisition (Shuster and Wade, 2003). Unlike viability selection, sexual selection is sex-specific and operates on variation in "mate-getting ability." In primates and most other animals, sexual selection largely operates on males (Shuster and Wade, 2003). Population structure plays a major role in determining the opportunities for sexual selection because male fitness is influenced by the spatial and temporal distribution of sexual rivals and females across a population (e.g., Kappeler, 1999; Pereira et al., 2000). Even simple indices of population structure such as the socionomic adult sex-ratio within groups can influence reproductive patterns among males. In an intraspecific analysis of *Propithecus verreauxi* reproductive success Lawler et al. (2003) found that the number of offspring sired by resident males decreased as the number of females within groups increased. One explanation for this pattern is that males cannot monopolize conceptions with all the females in their group as many of the paternities resulted from visiting males during the mating season (see Andelman, 1986) (Fig. 4B). Relative to the operational sex ratio, the socionomic sex ratio

is underemphasized in studies of sexual selection even though demographic models demonstrate its importance in shaping male and female reproductive strategies (Kokko and Jennions, 2008).

A study by Watts (2000) further illustrates the interplay between male reproductive strategies, life history variables, and socionomic sex ratio. Watts (2000) examined the reproductive consequences of different sociosexual strategies that characterize male mountain gorillas (*Gorilla gorilla beringei*). Similar to Janson (2003), Watts' demographic model was question specific and deterministic. Drawing from long-term data, nonsilverback males could be characterized as either "followers" or "bachelors." Followers often reach adulthood in their natal group and are subordinate to the dominant male. They have limited mating access to females, but followers can sometimes emerge as the dominant male in the group. Bachelors reach adulthood in groups that do not contain females, often by emigrating from their natal group, but may have mating access to females if females join their all-male groups. Both bachelors (in groups that contain females) and followers have limited mating access as subordinates, but followers have more mating access and have greater opportunities to increase inclusive fitness than bachelors. Watts developed a sociodemographic model of expected "offspring equivalents" that each type of male could expect to achieve over a given number of years. The model calculated expected fitness with respect to the following: the probability of becoming a dominant male, female group size, expected male tenure length in groups, group-size specific reproductive output, infanticide risk, breeding probability of followers with nondispersing daughters of dominant male, and indirect fitness gains that followers get from helping to defend against infanticide. Watts obtained values for these terms from empirical data. He explored different versions of the model with respect to female group size/composition and infanticide risk. His major results indicate that followers have much more "offspring equivalents" than bachelors, and this result is generally robust to variation in the values for each term (Fig. 4C). As Watts noted that, if bachelors do worse than followers, why do males disperse from their natal group to become bachelors? Likely, they do so if they are low in the "breeding cue" and the dominant male in their group is young (Watts, 2000). Similarly, followers are likely tolerated by dominant males because they can aid in infanticide defense. Watts suggests that variation in sociosexual strategies among males is determined by a combination of factors, notably population growth and density and the structure of social groups, which in turn influence the "decision" to become a follower or bachelor.

Fertility selection and dispersal. Fertility selection concerns variation in offspring production by sets of parents; in fertility selection models fitness values are assigned to a pair sexually reproducing parents and not to individuals. Though it is not often recognized, dispersal and emigration fall under the rubric of fertility selection because the evolution of sex-biased disersal and philopatry often results in viable outbred offspring from genetically unrelated parents (Chesser, 1991a,b). Dispersal and emigration are major determinants of spatial population structure. Based on years of empirical research, it is now clear that primate species have variable dispersal patterns and very few species can be neatly categorized into strict categories of female-philopatric or male-philopatric; instead species manifest sex-specific propensities of dispersal (Moore, 1993; Jack and Isbell, 2009). The hypotheses put forth to explain dispersal and philopatry include inbreeding avoidance, mating competition, enhancing mate quality, bet-hedging to maximize fitness across groups, as well as psychological factors (Moore, 1993; Charpentier et al., 2007). A demographic model of baboon dispersal illustrates the various factors that come into play with respect to dispersal "decisions."

Alberts and Altmann (1995) conducted an empirical and theoretical analysis of the costs and benefits of male dispersal in wild baboons (*Papio cynocephalus*). They first noted that the median age at dispersal from their natal group was 8.5 years and that median tenure length in nonnatal groups was 2 years. Half of the males in their sample were reproductively active in their natal group before dispersing. This allowed the researchers to look at the costs of reproducing in their natal group. They showed that infant mortality was relatively higher for natal sires than non-natal sires. Dispersal, however, also entails costs in terms of time spent alone because males miss out on reproductive opportunities and incur mortality through predation. These empirical results allowed Alberts and Altmann to construct a deterministic model of the demographic, ecological, and sociosexual factors that influence dispersal "decisions." They examined a series of variables that included survival of dispersing versus staying males (l_d vs. l_s), the proportion of time spent encountering mates in dispersing versus staying males (e_d vs. e_s), the number of mates attained by dispersing versus staying males (m_d vs. m_s), predation (high vs. low), and number of groups (N) in the population (i.e., density). N is inversely related to time spent alone, because at low density, males do not encounter mates as often as at high density. At low density, encounter rates (e_d) drop and survival probability (l) also decreases because males are spending more time alone and thus can die via predation. They showed that dispersal will be favored when $m_d/m_s > l_s/(l_d * e_d)$. Essentially, dispersal is favored over staying when the mates acquired by dispersing offset the costs of potentially dying (via predation) and encounter rate time. In their empirical data, the researchers could identify two types of males, successful or unsuccessful. If males were above (or below) median values for consortship activity relative to other males in their age class, they were designated as "successful" (or "unsuccessful"). Thus, they looked at the consequences of dispersal for successful versus unsuccessful males in terms of population density. Figure 4D shows the dispersal probabilities plotted against population density for successful versus unsuccessful males. At high densities, successful males have much to gain by dispersing since mate encounter rates are high and time spent alone is low; these males have a relative advantage over unsuccessful males in terms of dispersing and acquiring mates. At low population density, successful males incur a relatively higher cost to dispersing than unsuccessful males as they incur more lost mating opportunities (more time spent alone) than unsuccessful males. This model is particularly compelling because it examines dispersal probability in terms of survival, encounter rates, and mate acquisition, and it looks at how these factors alter dispersal probabilities as a function of population density. It also takes into account the fact that males differ in their phenotypic quality. Assessing female phenotypic quality and also

tracking offspring production/quality for unsuccessful versus successful males would help determine if fertility selection operates in this population.

This section considered the demographic factors that influence viability selection, sexual selection, and fertility selection. This section opened with the idea that behaviors can be studied with reference to their fitness consequences. In such cases, one picks a measure of fitness such as "offspring equivalents" or "mate acquisition" and writes this measure of fitness as a function of the relevant factors that are thought to influence fitness. This approach was embodied in the models developed by Watts, Janson, and Alberts and Altmann (Fig. 4). While these are deterministic models, the behavioral "options" available to individuals were, in part, determined by the behavior of other individuals. More generally, many of the behavioral strategies available to individuals depend on the frequency of other strategies played by individuals in the population. Game theory is used to analyze frequency-dependent behavioral strategies (Dugatkin and Reeve, 1998), but game-theory models are also deterministic. That is, once the fitness values and strategies are specified, the model output remains constant. No doubt, behavioral strategies are also likely to be influenced by stochastic demographic processes. Demographic stochasticity can alter behavioral strategies in ways that cannot be anticipated by frequency-dependent deterministic models (Rice, 2004). Documenting the impact of demographic stochasticity on behavioral evolution remains a key challenge for empirical and theoretical primatology. Altmann and Altmann's observation, made over 30 years ago, remains true today, "Effects on behavior of small-sample demographic variations are poorly understood, but the potential is enormous" (1979: 57–58).

Life history theory and demography

Demographic studies of vital rates. Life history theorists study how and why life cycles differ across species and which vital rate (or rates) might be key determinants of life cycle evolution. For example, adult mortality patterns are often viewed as a major determinant of life history schedules, as embodied in the work of Charnov (1993; Charnov and Berrigan, 1993). Similarly, the risks of juvenile mortality have been proposed to explain the relatively slow rate of growth among juvenile primates (Janson and van Schaik, 1993). Other models examine the age-specific fecundity function, $l(i) \times m(i)$, (see the life table description above) in the evolution of developmental shifts and fertility (Cole, 1954; Lewontin, 1965). Leigh and Blomquist (2011) provide an excellent summary of these models as they apply to primates. Many primatological studies of life history evolution have largely occurred without explicit reference to demography and population dynamics. Most studies have been comparative and pattern oriented; comparatively fewer studies have been population focused and process oriented. As discussed below, process-oriented studies of chimpanzees, mouse lemurs, and baboons illustrate the diverse demographic approaches to understanding the factors that shape important life history traits in wild primate populations.

Jones et al. (2010) conducted a demographic analysis on the determinants of fertility in Gombe chimpanzees (*Pan troglodytes*). They used 43 years worth of data on age-specific fertility and looked at numerous predictor variables that were thought to influence reproduction. Their analysis is relatively novel in that they included a term in their model pertaining to frailty. Formally, frailty describes the individual variation in susceptibility to death beyond what is determined by age or other measured variables (e.g., Vaupel et al., 1979; Vaupel et al., 1998); frailty can also be used to capture individual variation more generally. Jones et al. (2010) used a Cox proportional hazards model [see Eq. (10)] that took into account mother's age and dominance rank, sex and survival of the infant, and interbirth interval between first and second offspring. They also included a random effect in their model—mother's identity—which captured the degree to which a female's fertility was due to her own phenotypic quality (i.e., frailty). Using Akaike's information criterion (AIC), Jones et al. found that the best supported model contained age, first birth interval, binary rank (high versus all other ranks), and sex of previous infant as covariates. They found that mother's age had a significant effect on fertility, with older individuals having a reduced "hazard" for giving birth. Similarly, the loss of an infant had a major effect on subsequent births, increasing the hazard for giving birth by 134-fold. Mother's rank, when scored as high versus all other ranks, also positively influenced the birth hazard. Finally, phenotypic quality influenced the fit of the model; the random effect of individual phenotypic quality was a significant predictor of fertility. Jones et al. showed that there is large variation in individual fertility that cannot be explained by age, rank, parity, and other measured covariates.

Kraus et al. (2008) sought to model sex-specific survivorship in a wild population of gray mouse lemur (*Microcebus murinus*). Their main hypothesis was that males would show lower survivorship during the breeding season due to male–male competition and roaming. Taking into account recapture probability, p, (from above) they sought to estimate survival probabilities of males and females. Survival can depend on a lot of things. Individuals may differ in survival probability due to age and sex. Survival probability can also differ across seasons (e.g., winter vs. summer) or year. There can also be interactions and additive effects among these variables. Kraus et al. (2008) took all these factors into consideration and tested the fit of several different models to their data. Because the data involved the recapturing of live animals each season, their models also had to account for "trap shyness" (where individuals are recaptured less than expected on subsequent occasions) and "trap happiness" (where individuals are recaptured more frequently than expected on subsequent occasions), because trap dependence can bias survival estimates. They constructed numerous models in which the survival and recapture parameters were functions of age, sex, season, year, and trap happiness (for recapture probability only), and many of their models had additive and interactive effects among the factors. They ranked the fit of their models using AIC and used model-averaging techniques to get estimates of the sex-specific survival probabilities. The power of their analysis lies in the fact that they could statistically separate out age, season, sex, and yearly effects on survival while accounting for recapture probabilities. Consistent with their hypothesis, they found a lowered survival probability during the breeding season for males but not for females. Survival probabilities between the sexes did not differ during nonbreeding periods.

Brownikowski et al. (2001) modeled mortality patterns in wild and captive baboons (*Papio hamadryas*). Their

wild data came from two studies of baboons, one at Gombe National Park (Tanzania) and one at Amboseli National Park (Kenya); their captive data came from long-term records at the Southwest Foundation for Biomedical Research. Using census data, they first constructed life tables for each set of females to determine age-specific mortality, $u(i)$ (see life table analysis above). They fit parametric models to the mortality rate data. After testing both logistic and Gompertz models, they found that a Gompertz function better fit the data. Their basic model was $u(i) = \psi \exp^{\gamma i}$, where ψ is the baseline mortality at age 5, and γ is the exponential increase in adult mortality. They found an interesting pattern in their data when comparing the "shape" of the mortality function among populations. First, they found few differences in γ among the two wild and one captive populations of baboons; all populations appeared to die at the same age-specific rates (the captive population had a slightly slower rate). However, the baseline levels of mortality, ψ, differed among the populations indicating that total life expectancy differs among populations because the populations "start off" with different baseline levels of mortality. More simply, they found similar rates of mortality (i.e., slopes) but different baseline mortality (i.e., intercepts). Following Vaupel et al. (1979), they interpret the ψ parameter as a measure of the average frailty of the population. A variety of environmental factors can influence ψ. Ecological (and captive) conditions can create situations where baseline mortality is altered due to the presence or absence of predators and/ or abundance of food. The authors also noted that genetic mechanisms are likely to play a role in frailty, since ψ has been shown to be heritable in these populations. Bronikowski et al. (2001) speculate that individual differences in life span and risk of death are primarily due to differences in frailty.

The summaries above give a sense of the diversity of approaches for understanding life history evolution using demographic models and data. Many of the studies outlined above used long-term data and/or developed age-structured population models. However, it is also possible to gain insight into life history evolution using minimal demographic data. Ross (1988) was one of the first to apply these "reduced" models to primates. A similar approach was used by Blomquist et al. (2009) in their exploration of platyrrhine life history patterns; they used a demographic model developed by Charlesworth (1994). The model is as follows

$$l_\alpha b \frac{\lambda^{-\alpha}}{1 - P\lambda^{-1}} = 1 \qquad (11)$$

where α is age at first reproduction, l_α is the percentage of newborns surviving to age α, b is the birthrate, P is the annual survival of adult females, and λ is the population growth rate (technically, this is an age-based MPM that assumes constant fertility and an infinite number of adult age classes with constant survival; Skalski et al., 2005). Values for the reproductive parameters were drawn from the literature (both captive and wild) and the equation was solved for λ using a simulation. They determined the elasticity of λ to the parameters by implicit differentiation. They found that λ was most sensitive to adult survival. Their analysis highlights, among other things, the fact that even minimal demographic data can provide insights into life history evolution. Along these lines, Godfrey et al. (2002) were

able to extract demographic data from fossil samples to study the demography and selection pressures in extinct subfossil lemurs.

Future directions in the demographic study of life history evolution. A key equation that helped unite life history evolution with demography was derived by Lande (1982),

$$\Delta \bar{a} = \frac{1}{\lambda} \mathbf{G} \nabla \bar{\lambda} \qquad (12)$$

where,

$$\nabla \bar{\lambda} = \begin{pmatrix} \frac{\partial \bar{\lambda}}{\partial \bar{a}_{11}} \\ \frac{\partial \bar{\lambda}}{\partial \bar{a}_{12}} \\ \vdots \\ \frac{\partial \bar{\lambda}}{\partial \bar{a}_{ij}} \end{pmatrix}$$

Lande showed that the mean change in a set of vital rates, **a**, is determined by the selection gradient ($\nabla \bar{\lambda}$) acting on each vital rate (this is a vector of partial derivatives of mean fitness with respect to each vital rate, a_{ij}), multiplied by the genetic variance–covariance matrix, **G**. In essence, the vital rates change across generations due to selection pressures as well as the additive genetic variance/covariance underlying the vital rates (see Lawler and Blomquist, 2010). While this equation is important for uniting demographic and evolutionary change, there have been very few attempts to estimate all the terms in this equation from a single population (Pelletier et al., 2007).

Lande's equation [Eq. (12)] intimates several outstanding questions in primate life history evolution. 1) *Which vital rates are currently under selection?* As shown in Table 1, many studies show that adult survival is under strong directional selection. Getting to adulthood is key, but there are diverse ways to reach adulthood (Pereira and Leigh, 2003; Leigh and Blomquist, 2011). Relative to other mammal species primates grow slowly (Pereira, 1993). Determining the ecological, demographic, and social mechanisms that lead to key shifts in the rate and timing of developmental milestones can help flesh-out how growing juveniles to become successfully reproducing adults. Sensitivity/elasticity analyses can suggest what evolutionary "pathways" are available to selection in terms of modifying juvenile growth rates/patterns in the transition to adulthood. Further, little is known about patterns of stabilizing selection acting on the vital rates. Some empirical and theoretical work suggests that stabilizing selection should act on survival in younger animals whereas fertility should be under stabilizing selection in older animals and under disruptive selection in younger animals (Caswell, 1996; Kirkland and Neuman, 1994) but these patterns of selection are rarely documented in wild primate populations (cf. Lawler, 2009). 2) *What are the ecological, social, and demographic mechanisms that produce variation in vital rates?* There has been much progress in determining how things like rainfall, food abundance, dominance rank, dispersal, and mate acquisition influence key life history traits. These data provide a mechanistic context to the patterns of selection acting on life history traits. Given that adult survival plays such a strong role in determining the pattern of selection on the life cycle more studies are needed to document sources of

mortality in primates. At present, the relationship between extrinsic mortality and senescence is unclear. One potential avenue of research is to search for ecological variables that reduce extrinsic mortality (e.g., Williams et al., 2006; Shattuck and Williams, 2010). However, it is perhaps not a matter of documenting sources of extrinsic mortality per se, but the age-specific patterns of extrinsic mortality, as only the latter are responsible for changing the selection gradients that influence the rate of senescence (Abrams, 1993; Caswell, 2007). Mortality patterns in primates do not show any phylogenetic trends (Bronikowski et al., 2011), so more field-based studies of the ecological mechanisms that underlie survival and mortality are warranted. 3) *What are the patterns of phenotypic variation/covariation and autocorrelation among the vital rates?* The selection gradient in Eq. (12) can be rewritten as $\nabla \lambda = \mathbf{P}^{-1} \operatorname{Cov} [w(\mathbf{a}), \mathbf{a}]$, where $\mathbf{P}^{-1}$ is the matrix inverse of the phenotypic variance/covariance matrix of the vital rates and $w(\mathbf{a})$ represents the fitnesses of a vector of vital rates, $\mathbf{a}$, (Lande, 1982). The important point here is that it pays to know how the vital rates phenotypically covary as embodied in the $\mathbf{P}$ matrix. The patterns of covariation as well as serial correlation across years in the vital rates has likely played a major role shaping life history patterns across species (Tuljapurkar et al., 2009; Morris et al., 2011). 4) *How much additive genetic, environmental, cohort, and maternal variation/covariation do the vital rates manifest?* The $\mathbf{P}$ matrix of vital rates can be decomposed into genetic and environmental sources of variation/covariation, $\mathbf{P} = \mathbf{G} + \mathbf{E}$. To the extent possible, it is important to document the additive genetic correlations that might be found among vital rates. There have been scant attempts to estimate these correlations in wild primates, but a notable study was conducted by Blomquist (2009) who documented a genetically mediated trade-off of age at first reproduction and survival in Cayo Santiago macaques. In principle, the $\mathbf{G}$ and $\mathbf{E}$ matrices can be further decomposed into additional sources of covariation, including cohort and maternal variation. Cohort variation occurs when some of the variation in vital rates is due to birth year, while maternal variation occurs when some of the variation in vital rates is due to siblings sharing the same mother. Cohort effects are likely pervasive and important with respect to primate population dynamics, but they are rarely explored in wild primates (but see Altmann, 1991). Maternal effects also likely operate in primate populations (e.g., Altmann and Alberts, 2005) but their effects on population dynamics are poorly documented.

Population genetics and demography

In this section, I review some population genetic studies of population structure and dynamics in wild primates. In particular, I focus on the concepts of genetic subdivision and effective population size. For many primate species, group-living creates genetic subdivision in a population and genetic variation within and across social groups has important implications for kin selection and social evolution. Effective population size is an important concept that helps determine the amount of genetic change a population will experience as it evolves through time. While the topics discussed in this section do not exhaust the ways in which population genetics and demography intersect (see Charlesworth, 1994), they highlight the ways in which genetic structure and genetic change interact with demographic population structure and population dynamics.

Population structure. Population geneticists have long been interested in how patterns of migration, mating, and new group formation influence the genetic structure of populations. Often population structure is nested and can be arranged hierarchically, such as subunits or demes within a larger population. Wright's F-statistics are one of the most widely used measures for determining how genetic variation is apportioned among different nested levels of a population. The statistics can be derived using a variety of approaches but are most often used to measure the correlation between alleles in individuals relative to the subunit (F_{IS}); the correlation of alleles in individuals relative to the total population (F_{IT}); and the correlation of alleles in a subunit relative to the total population (F_{ST}) (e.g., Sugg et al., 1996). When population subdivision has an apparent geographic organization, it is possible to measure the amount of genetic differentiation between population subunits in different areas using F_{ST}. Here, population subdivision is interpreted as the genetic distance between subunits due to the degree of drift experienced by each of the randomly mating subunits. Theoretical expectations arising from this type of geographic subdivision suggest that semi-isolation among subunits will lead to increased F_{IS} and F_{IT} values due to the correlation of homologous alleles within the subunits through time (Wright, 1978). More simply, genetic differentiation among subunits is assumed to arise from quasi-isolation among these units ($F_{ST} > 0$) and thus individuals within each unit become inbred over time ($F_{IS} > 0$), as does the total population ($F_{IT} > 0$). Storz (1999) has noted that this explanation was assumed to characterize mammalian social groups; many population geneticists often viewed mammal populations as organized into small, semi-isolated, panmictic social units that retain high levels of inbreeding due to limited dispersal. However, defining population units on the basis of geography or some other external criteria can cause erroneous pooling of genetically distinct population units. In this case, if the population subunits are defined without respect to breeding structure, mating, and/or sex-biased dispersal, F-statistics will underestimate the amount of genetic variation at all population levels (Sugg et al., 1996). More to the point, population genetic models such as Wright's F-statistics need to incorporate demographically realistic factors if they are to explain patterns of genetic variation in spatially complex age-structured populations such as primates.

Wright's F-statistics have been rederived by Chesser (1991a,b) to account for sex-biased dispersal and philopatry, the presence of reproductive and nonreproductive members in social groups, and reproductive skew. Chesser showed that under the more realistic conditions of female philopatry, male dispersal, and male reproductive skew, a very different pattern of genetic variation emerges within and among social groups in a population. In this situation, social groups tend to become fixed for different alleles, resulting in high genetic variation among groups ($F_{ST} > 0$), but this genetic variation is not due to limited gene flow among groups but rather to the presence of matrilines due to female philopatry (due to different gene correlations among the matrilines). Further, when a male from one matriline disperses and mates with females from another matriline, he brings with him alleles from his mother's matriline. Upon

mating with females from a different matriline (and characterized by different alleles), all the offspring of this union will be heterozygous, creating highly outbred offspring ($F_{IS} < 0$). Thus, a primate population can be characterized by a fair amount of genetic subdivision ($F_{ST} > 0$) but offspring within social groups will not be inbred. This pattern of genetic differentiation has been found in numerous primate species, including *Alouatta seniculus* (Pope, 1992), *Macacca mulatta* (Melnick et al., 1984), *Macaca fuscata* (Aoki and Nozawa, 1984), and *Propithecus verreauxi* (Lawler et al., 2003).

Because primate populations are structured by sex and age, the patterns of genetic variation within and among social groups differ in males and females as well as adults and offspring. When females remain in their natal group, gene correlations build up among females but different groups are fixed for different alleles. On the other hand, males disperse from their natal group, and this usually scrambles any potential gene correlations among males across groups. In this case, it is expected that F_{ST} FEMALES > F_{ST} MALES, since gene correlations among males are broken up by male dispersal, as found in *Propithecus verreauxi* (Lawler et al., 2003). This pattern will be reversed in species with female-biased dispersal, as speculated for *Papio hamadryas* (Hammond et al., 2006). Genetic differentiation also differs for adults versus offspring but the pattern of genetic differentiation depends on the population wide sex ratio of offspring born into the population, as well as philopatry and reproductive skew. Under strong polygyny and female philopatry, offspring cohorts within groups are united by paternal and maternal alleles, so that average relatedness within cohorts is high. Across a population different offspring cohorts share different sets of paternal and maternal alleles resulting in higher genetic differentiation than adults (F_{ST} OFFSPRING > F_{ST} ADULTS). Under weak polygyny and female dispersal, offspring cohorts within groups share few alleles in common. This results in a pattern of genetic differentiation among offspring cohorts that differs little from adults (F_{ST} OFFSPRING = F_{ST} ADULTS). The sex ratio of offspring can also influence patterns of genetic correlations among adults and offspring. In a female philopatric species, if more females are born into social groups than males, female cohorts remain in their natal group as they recruit into adulthood and gene correlations among these cohorts will remain in place. If more males are born into social groups than females, the gene correlations among offspring cohorts will be rearranged due to male dispersal into neighboring groups. Thus, any gene correlations among male offspring cohorts will be broken up as they disperse, a pattern documented in *Propithecus verreauxi* (Lawler et al., 2003).

The processes of new group formation also influence genetic population structure. Group formation falls along a continuum of the random aggregation of unrelated individuals to nonrandom group fissioning along lines of kinship. Fission along lines of genetic relatedness, such as when two matrilines split to form two new groups, results in a high degree of genetic differentiation among groups; however, when new groups form from unrelated sets of parents then genetic differentiation will not be increased among social groups. Genetic subdivision in a population may be enhanced or diminished depending on the degree of reproductive skew and the rate of new group formation. When there is high-reproductive skew in a group that later splits, then fissioning along matri-

lineal lines will not greatly enhance genetic subdivision. This is because offspring cohorts belonging to different matrilines in the daughter groups will be united by paternal alleles (Melnick and Kidd, 1983). This pattern has been documented in Cayo Santiago macaques (Melnick, 1987). The rate of new group formation also influences genetic subdivision. Pope (1992; 1998) shows that red howler monkeys (*Alouatta seniculus*) form new groups by solitary males and females. Matrilineal relatedness increases over time in these groups whenever daughters remain in the group with their mother. In this case, established groups are characterized by a higher average relatedness relative to newly formed groups. Average relatedness within groups is proportional to genetic variation between groups (Hamilton, 1971). In a growing population, where the rate of new group formation is high, the rate of new group formation will be inversely related to the genetic differentiation between groups, as most new groups will contain relatively low average relatedness. However, in a growing population where new groups are formed along lines of kinship (and not by solitary individuals), genetic differentiation is expected to be pronounced as daughter groups contain high average relatedness (Pope, 1992; 1998; Storz, 1999).

The demographic processes of sex-biased dispersal and new group formation, coupled with reproductive skew, have important implications for the evolution of kin selection. For selection to act at any level (genes, individuals, groups, and species) selection requires multiple units at that level and variation among the units (Rice, 2004). Kin selection requires variation among sets of individuals who either share identical-by-descent (IBD) genes or do not share IBD genes. Genetic correlations among individuals within a group provide an impetus for kin selection to act. However, as shown above, several demographic and behavioral factors interact to make some genetic correlations among individuals more permanent than others; these include the processes of new group formation, the population-wide offspring sex ratio, sex-biased dispersal patterns, and reproductive skew. As should be evident from the brief discussion above, important insights into social evolution can be gained by examining biparentally inherited autosomal loci in the context of demographic population structure; additional insights can be gained by simultaneously analyzing uniparentally inherited markers (e.g., Langergraber et al., 2007; Di Fiore, 2009) and studying these effects across broader geographic scales (e.g., Arora et al., 2010).

Population dynamics. One of the most important concepts that unites population dynamics and population genetics is effective population size (N_e). With few exceptions, effective population size—as opposed to census population size—is often the thing that matters when attempting to understand how evolutionary forces shape populations through time. N_e dictates the intertwined dynamics pertaining to the efficiency of selection, the impact of drift, the fixation probability of deleterious and beneficial alleles, the degree to which a population may respond to selection, and inbreeding depression (Rice, 2004; Hedrick, 2005; Allendorf and Luikart, 2006). N_e can be calculated in a variety of ways with respect to the loss of heterozygosity (N_{ei}) or sampling variance in allele frequency (N_{ev}) based on a consideration of demographic factors. Other conceptualizations of N_e include the coalescent effective size, which is related to N_{ei}, and the

eigenvalue effective size, which is related to N_{ev}. Historical estimates of N_e, based on coalescent effective size, have been recently estimated for a variety of primate populations (e.g., Storz et al., 2002b; Goosens et al., 2006; Bonhomme et al., 2008). All of these types of N_e keep track of how genetic variation is lost and/or reapportioned in a population.

There are several good reviews of effective population size that provide some basic estimates of N_e under the assumptions of unequal numbers of males and females, unequal family size, and fluctuating population size (e.g., Hedrick, 2005); all of these criteria likely apply to primate populations. However, many primates are also characterized by the following demographic properties: reproductive skew, social groups, overlapping generations, long generation times, and long lifespans. These factors have been shown to influence estimates of N_e (e.g., Nunney, 1993; Chesser et al., 1993; Lotterhos, 2011). As Table 1 shows, many primate species are characterized by long generation times, so a brief exploration of the influence of generation time on N_e is warranted. Nunney (1993) derived an equation for calculating the influence of overlapping generations, generation time, and reproductive skew on effective population size,

$$N_e^v =$$

$$\frac{4r(1-r)NT}{([A_m(1-r)+A_f r] + [I_{bm}(1-r)+I_{bf}r] + [A_m I_{Am}(1-r)+A_f I_{Af}r])}$$

(13)

where r is the proportion of males, N is population size, T is generation time, A refers to the average male and female life span (subscripted accordingly by m and f), I_A is the standardized variance in lifespan (subscripted accordingly by m and f), and I_b is the standardized annual variance in reproductive success in males and females (subscripted accordingly by m and f).

There have been very few estimates of N_{ev} in primate populations that take into account generation time, overlapping generations, and reproductive skew (see Pope, 1996; Storz, 2002a). Using demographic and census data from the on-going study of wild sifaka (*Propithecus verreauxi*) (e.g., Lawler, 2007; Lawler et al., 2009), I calculated the N_{ev} for this population across 4 years using Eq. (13) above. The standard equation that calculates N_{ev} due to reproductive skew is: $N_{ev} = 4N/V + 2$, where V denotes variance in reproduction (Wright, 1938). However, this equation does not take into account overlapping generations or generation time. One can see that if V is 0, then the effective population size is twice the census size (N). As V increases, N_{ev} goes down; for example, when $V = 5$ and $N = 100$, then $N_{ev} = 57$. When generations overlap, however, the variation due to reproductive skew is minimized. Across a wide range of mating systems and differences in reproductive skew, N_{ev} increases as generation interval increases. In the example from sifaka, generation intervals are about 17–19 years (Lawler et al., 2009; Morris et al., 2011). Sifaka are characterized by an average age of first birth of 6.5 years and an average adult life expectancy of about 20 years (Morris et al., 2011; Lawler, unpublished data). These two values combined with the long generation interval allow for many sexually mature males to enter into the population each year. Any sampling variance caused by reproductive skew within a breeding season is mitigated by the fact that offspring alleles may
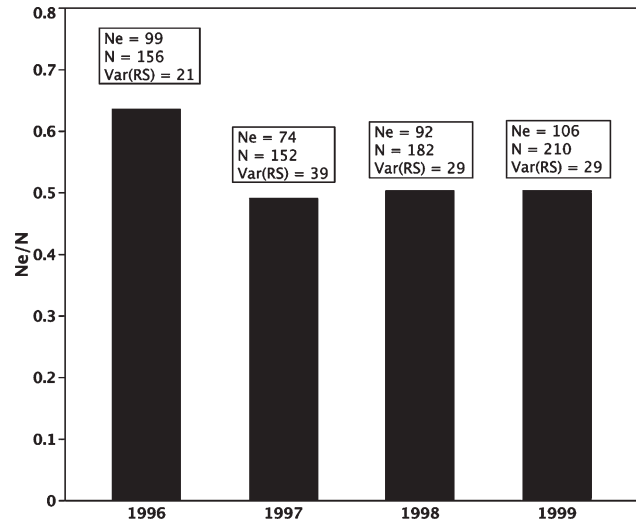
Fig. 5. Values for the ratio of census size to effective population size (N_{ev}/N) in Verreaux's sifaka over a 4-year period. Effective population size was calculated taking into account reproductive skew (Var(male RS)), overlapping generations, generation interval, and census size (N). See text for discussion.

come from adult males who may have sired offspring in different breeding seasons. High variation in male reproductive success can lead to potentially high disjunctions between N and N_{ev}. However, because of the long generation time and extended reproductive career in male sifaka, a larger sample of male gametes are sampled from the pool of potential male parents, as male reproductive periods are shorter than generation time. The overall effect of overlapping generations, as measured by the generation interval, is to increase the N_e/N ratio as generation time increases (Nunney, 1993). Sifaka fall within the range of $N_e/N = 0.5$ as predicted by Nunney based on theoretical considerations; this value is largely independent of differences in the variation in male reproductive success and census size (Fig. 5).

N_e is a key parameter that tells us how a population will experience drift given some particular biological circumstance that violates one or more of the assumptions of an "ideal population." The stochastic processes that influence genetic variation due to drift come from two sources. The first source is the effects of Mendelian segregation on heterozygotes. The second source is effects of random reproduction. The first source is genetic and the second source is demographic. It is no wonder that many calculations of N_e include both genetic and demographic terms. Often it is argued that demographic processes take precedence over genetic processes with respect to most conservation decisions (e.g., Caughley, 1994). In some ways, this makes sense since extinction is ultimately a demographic process. However, as Nunney (2000) conveys, there are myriad genetic factors that influence extinction. These include the detrimental effects of inbreeding, the accumulation of deleterious mutations in small populations, and the lack of selection response to changing selection pressures (Burger and Lynch, 1995; Frankham, 1995; Lynch et al., 1995). All of these processes rely on the inverse relationship between genetic variation and extinction risk. As such, N_e provides insight into standing levels of genetic variation and it therefore provides a window into the genetic

processes that contribute to demographic extinction and persistence.

Conservation biology and demography

With its focus on key parameters that govern the growth or decline of populations, demography has natural ties to conservation biology. This section reviews demographic theory as it applies to conservation problems. As Soule (1985) points out, conservation biology is both a multidisciplinary enterprise as well as a "crisis discipline." Regarding the latter, Soule (1985) suggests that conservation biology is a discipline that requires quick action. Conservation biologists do not have the time to hypothesize and test numerous conservation alternatives. They must act quickly. Demographic techniques can supply relevant information about the viability of particular populations, and thus, they can contribute to conservation decisions. Caswell (2001) suggests that conservation problems are best tackled with an analogy to medicine. That is, for any particular conservation problem, it is necessary to make an assessment, a diagnosis, a prescription, and a prognosis. I follow Caswell's framework (2001) as a means to organize this section; I then discuss some take-home messages regarding demography and conservation.

Assessment. Assessment involves the estimation of population growth rates and net reproductive rates. These indices provide critical information on whether the population is growing or shrinking. The International Union for Conservation of Nature (IUCN) criteria for listing species as vulnerable, endangered, or critically endangered utilize population growth rate as well as indices of habitat fragmentation and abundance (Cowlishaw and Dunbar, 2000). In this regard, population growth rate, λ, helps assess extinction risk. Many studies have estimated population growth rate in wild primate populations. These estimates come from "simple" counts of animals from time step to time step, with no attempts to model recapture probability, and they also come from the use of life tables, MPMs, and other analytical techniques (Table 1). For example, Strier et al. (1993) censused individually recognized animals in a group of Muriquis (*Brachyteles arachnoides*). Over a 9-year period, they observed the number of animals in the social group to increase from 22 to 42 animals, due to a high birth rate and high infant survival. This is a remarkable increase in population numbers. The population growth rate over these 9 years is calculated as $\lambda = 42/22 = 1.9$, and the average annual growth rate is $\lambda = 1.9^{1/9} = 1.07$ (the population is growing by 7% per year). As another example, Lawler et al. (2009) used a stage-based MPM to determine the annual population growth rate in a population of Verreaux's sifaka, *Propithecus verreauxi* (Fig. 2C shows the life cycle graph). Based on censuses of individually marked animals, they were able to generate information on survival, growth, and reproduction. They used mark-recapture methods to formally account for missing animals and thus estimated the vital rates as well as resighting probabilities. From their five-stage MPM, they generated an annual population growth rate of $\lambda = 0.98$, with 95% confidence intervals ranging 0.95–1.003. The growth rates for muriquis and sifaka suggest that these populations are not in imminent danger, though the point estimate for sifaka suggests this population is declining by 2% per year.

Diagnosis. There are many methods for diagnosing the causes of population decline in wild primates, the most basic being a simple observation of the factors that increase mortality among individuals. These types of observations are critical to diagnosis, but they are not explicitly demographic. The general demographic approach to diagnosing a population in peril is to assess the factors that contribute to variation in population growth rate and/or the vital rates of the population. For age- and stage-structured populations that are modeled using Leslie or stage-based matrices, assessing variation in population growth rate involves a life-table response experiment (LTRE). As noted by Caswell (2000: 621), a LTRE, "...looks back at an observed pattern of vital rates and asks how that pattern has affected variation in λ. The factors causing the variation in vital rates can be thought of, in very general terms, as 'treatments' in an 'experiment.'" There have been very few LTREs conducted on wild primate populations. Lawler (2011) conducted a LTRE on a wild population of Verreaux's sifaka using the life cycle in Figure 2C. He sought to determine how variation in the vital rates contributed to variation in population growth rate. Referring to the coefficients on the life cycle in Figure 2C, he found that the largest variation among life cycle transitions is for transition P5, and the largest covariation among entries is for G2/P5. This suggests that a major source of variation in λ is due to variation in the "ability" of stage 5 animals (in this life cycle stage 5 refers to "experienced mothers," see Lawler et al., 2009) to remain in this stage from year to year. Stage 5 also manifested covariation with other stages in terms of its contribution to variation in λ. The causes for these covariations need to be explored further but they allow conservationists to focus on the socioecological factors that create variation in vital rates and how this variation contributes to variation in population growth rate. A related analysis by Morris et al. (2011) examined the influence of variation, covariation, and serial correlation in the vital rates for six primate species (see Table 1 for species in their analysis). Morris et al. (2011) demonstrate that the variation in vital rates is remarkably minimal and does not show correlations with life history traits, body mass, or rainfall. They suggest that encephalization and/or omnivory allows primates to maintain fairly constant vital rates across years, particularly adult survival, in the face of stochastic environments. In essence, these primate species do not show variability in the vital rates that tracks any obvious biological or climatic factors. Instead, it is possible that dietary generalism buffers primate populations from perturbations that might be detrimental to dietary specialists. And in some species the social transmission of "survival knowledge" might also account for minimal variation survival rates.

Prescription. If a population is in rapid decline and the causes of its decline have been diagnosed, the next step is to prescribe a conservation tactic. Sensitivity/elasticity analysis is a powerful demographic technique for helping to prescribe management tactics. Sensitivity analyses can identify which age/stage classes have the most impact on population growth rate. For example, Dunham et al. (2008) constructed a three-stage MPM for Milne Edward's sifaka (*Propithecus edwardsi*) to explore the effects of climate, hunting, and deforestation on the viability of this species. They had stages corresponding to yearling, juveniles, and adults, where the latter two

stages had "self-loops" that allowed animals to remain in these stages from year to year. They parameterized their model using census data from two populations inhabiting Ranomafana National Park. They found that population growth rate is most sensitive to adult survival and fecundity, and that hunting of adult animals is expected to severely influence the viability of this population. As another example, Blomquist et al. (2009) conducted an elasticity analysis on selected platyrrhine species. These authors also found that perturbations in adult survival would produce the largest changes in population growth rate. They also noted that perturbations to age at first reproduction has a low impact on λ, suggesting that any factor that causes individuals to reach sexual maturity sooner (e.g., provisioning or a plentiful food supply) is not going to have much of an effect on the demographic health of the population. Almost all studies listed in Table 1 show that λ is most sensitive to adult survival. From a conservation standpoint, those primate populations that incur high adult mortality, for example, through targeted-hunting of adults (e.g., Peres, 1991), are the populations that will become the most inviable.

Prognosis. While sensitivity analysis provides a prescriptive framework to determine those life cycle transitions that have the greatest impact on λ, a population viability analysis (PVA) is used to make a prognosis for the threatened population (Boyce, 1992; Bessinger and McCullough, 2002). PVAs are a way to assess the probability of extinction of a population using a variety of demographic, ecological, and environmental data. Population projection is a simple form of a PVA. When habitat factors are taken into account, then such analyses are called population and habitat viability analyses. Cowlishaw and Dunbar (2000) provide an excellent summary of PVA analyses and their application to primates. Many PVA for wild primates use specialized programs such as VORTEX (Miller and Lacy, 2005) to assess the probability of extinction based on a wide variety of factors. A comprehensive PVA of orangutans in Borneo and Sumatra was conducted by Marshall et al. (2009; also see Bruford et al., 2010). Their analysis included inbreeding depression, environmental influences on reproduction and survival, density dependent effects on reproduction, mating system, reproductive skew, environmental catastrophes (such as fires, landslides, diseases, and el nino effects), hunting, logging, and a variety of life history and demographic factors (e.g., survival, age at first reproduction, sex ratio at birth, etc.). The values for these variables and parameters were based on a judicious consensus of numerous researchers. Some of their major findings include the following. If population sizes are initially small, such as 50, then orangutan population size will fluctuate over time and many simulations predict extinction within 1,000 years. If population sizes are above 250, then there are fewer fluctuations over time and populations are expected to persist over 1,000 years. The researchers also examined the influence of hunting and inbreeding in Bornean orangutans and the influence of hunting in Sumatran orangutans. Inbreeding depression was not a major factor contributing to extinction. When extra mortality was added to all age-classes due to hunting, they demonstrated that an additional 2–3% mortality rate due to hunting produced extinctions that were independent of habitat quality. Logging had a major effect on the viability of Sumatran orangutans. Moderates rates of habitat loss of about 5–10% result in extinction within 100 years or so. Current rates of logging are estimated to be 2–20% so their prognosis does not bode well for orangutan viability.

Demography and conservation: Some conclusions. Several take-home messages are worth emphasizing with respect to conservation biology as it intersects with demography. First, "conservation biology" is an oxymoron of sorts. That is, for a field where "biology" is nominally prominent, all threats to wild primate populations come from direct or indirect human activities such as hunting or habitat destruction. No matter how much demographic or biological data are collected from wild primate populations, their conservation will principally depend on changing the social and economic habits of humans. In this sense, the "biology" of a population constitutes a small portion of the larger conservation problem. In some cases, given the rate at which habitats are being destroyed, conservation biologists might better spend their time trying to change human behaviors and policies rather than collect demographic data for a PVA. That said, even if minimal demographic data are available it is clear that they can provide helpful information about the viability of primate populations (Dobson and Lyles, 1989; Blomquist et al., 2009).

Second, population growth rate, λ, is a strong predictor of the viability of the population. However, population growth rate alone does not provide information about the size of the population. In this regard, a small population with a positive population growth rate might still go extinct due to demographic or environmental stochasticity. Obviously, population growth rate should not be the sole source for making conservations decisions, and other demographic data should be included if they are available. Caswell (2001:615) shows that population growth rate, when calculated from a time-invariant model (where the vital rates are constant), correlates well with other estimates of population growth rate derived from models that include demographic and environmental stochasticity, density dependence, temporal variation, and dispersal. Thus when data are not available to calculate more realistic measures of population growth rate, a simple time-invariant estimate of population growth rate will still provide helpful information.

Third, while sensitivity values provide useful data on potential management targets, this information cannot always be put into practice. All sensitivity/elasticity analyses for primate populations suggest that population growth rate is most sensitive to adult survival. At first blush, this suggests that increasing adult survival is a simple way to increase the viability of primate populations. However, as pointed out by Blomquist et al. (2009), increasing adult survival might be biologically impossible if the majority of adults are dying via senescence and not extrinsic factors such as hunting. Similarly, implementing any sensitivity analysis might be economically infeasible even if it seems demographically beneficial. Nichols and Hines (2002) provide a method in which they mathematically combine an elasticity analysis along with a management option and a dollar amount for the cost of the management option,

$$m(\theta) = \frac{\partial \log \lambda}{\partial \log \theta} \frac{\partial \log \theta}{\partial x} \frac{\partial x}{\partial y} \qquad (14)$$

In their equation, $m(\theta)$ reflects the proportional change in λ given a perturbation to a vital rate θ, as well as the

cost of the management option. The first term is the elasticity of λ to a vital rate θ, the second term is the proportional change in the vital rate given some management option x, and the third term is the cost, y, of implementing the management option x. Apart from cost, it should be obvious that if one vital rate is difficult to modify (e.g., adult survival), it might be possible that another vital rate corresponding to the next highest sensitivity value is capable of modification (e.g., survival to sexual maturity) and that this modification will still produce a beneficial result. However, it is important to keep in mind that the vital rates themselves are often correlated, thus a perturbation to one vital rate may cause a change in another vital rate. Suffice to say, sensitivity/elasticity analyses should be applied judiciously.

Fourth, all demographic models are only as good as the input data. Sparse or poorly sampled input data will produce a set of results that might not be useful for making conservation decisions as argued forcefully by Struhsaker (2008). In addition, many prepackaged PVA programs have subroutines that can incorporate factors such as inbreeding, habitat destruction, density, and other factors into the analysis. It is unclear, at least for primates, if all of these factors need to be included into a single analysis. Researchers might feel compelled to include a value for a given factor (e.g., inbreeding) just because the program has included it as an option. This might lead to a misguided emphasis on a particular factor based solely on the model's output rather than an empirical investigation of how that factor actually impinges on primate populations. Finally, demography operates at the population level. With respect to conservation, demographic analyses do not tell us the individual circumstances of why animals might have perished. They can only summarize the population-level consequences of individual imperilments. In this regard, conservation "in the field" is necessary to provide a socioecological and anthropogenic context for why a population is declining in numbers.

CONCLUSION AND FUTURE DIRECTIONS

Demography focuses on the important biological events in the lifecycle of a species and analyzes these events to determine population structure and dynamics. As Figure 1 illustrates, demographic studies are increasing with respect to primates. This review has only scratched the surface of demographic concepts and techniques that have been applied to wild primate populations. Demographic analyses can also be extended in other ways that were not discussed above. A brief discussion of these extensions will highlight some of the remaining challenges in primate demography.

One important extension is density effects. Most demographic analyses can incorporate density effects by writing one or more vital rates as a function of the size of the population or social group. Population density plays a major role in determining mating strategies and shaping dispersal. However, density is often measured qualitatively in primate populations (e.g., high vs. low). It would be beneficial to get quantitative estimates of population density to determine how a range of continuous density effects influences behavioral strategies and population dynamics. Another extension that deserves much more attention is two-sex models. The usual assumption in most demographic analyses is that λ is determined by female fertility because there are always enough males

to fertilize each female. Two-sex models are constructed when there are differences in the vital rates among males and females. Often two-sex models lead to new insights into life history evolution when compared to female-based models (e.g., Rankin and Kokko, 2006; Tuljapurkar et al., 2007; Jenouvrier et al., 2010). Third, it is necessary to account for individual variation in demographic models since individual differences in fitness provide the raw material for natural and sexual selection (cf. Caswell, 2011). One method, as discussed above, is to include a term for frailty. IBMs constitute another route for exploring individual variation. Additional techniques are discussed in McGraw and Caswell (1996), Link et al. (2002), Coulson et al. (2006), and Tuljapurkar and Steiner (2010). Fourth, there is a vast theoretical literature about the how vital rates are expected to change and evolve under stochastic environments and fluctuating population size (e.g., Caswell, 1982; Tuljapurkar, 1990; Caswell, 2001; Roff, 2002; Lande et al., 2003; Metcalf and Koons, 2007). More empirical estimates of vital rates are required from wild primates to test the theoretical expectations of these models. Fifth, few demographic studies of primates formally incorporate recapture/resighting probabilities into estimation procedures, nor do they report statistics of uncertainty in parameter estimates such as confidence intervals. This can lead to erroneous biological conclusions and can be particularly problematic when making a conservation decisions. Finally, more data and models are needed to understand the behavioral, ecological, and anthropogenic factors that create population structure. In particular, more attention should be directed at defining "a population" versus "a metapopulation." Primate habitats are increasingly fragmented and disturbed (Harcourt and Dougherty, 2005) and such disturbances can lead to changes in social structure, behavior, abundance, and possibly vital rates of groups living in these different areas (reviewed in Cowlishaw and Dunbar, 2000).

In this review, I have discussed how individual schedules of survival, recruitment, and fertility can be collectively analyzed for their demographic consequences. The ensemble of individual schedules provides the vital rates of the population—the primary components of fitness that govern population dynamics and contribute to population structure. In this respect, demographic traits, as embodied in the vital rates, are both targets and agents of evolutionary change. Acquiring data on vital rates from wild primate populations is necessary for understanding a variety of questions concerning behavioral ecology, life history theory, population genetics as well as conservation strategies. After all, both biological and human factors impact on the vital rates to produce a demographic response. Analyzing these impacts can illuminate both the processes of biological evolution as well as how these factors may be altered to produce a desirable conservation strategy. However, in slowly maturing, age-structured populations such as primates, information on vital rates from wild populations is rarely available. As shown in Table 1, primate generation times are quite lengthy; consequently, estimating age- or stage-specific fertility and survivorship requires continuous, long-term monitoring in the field. The key challenge for primatologists thus involves the collection of sufficient demographic data such that the parameter estimates in their demographic models are statistically robust and capable of informing conservation strategies.

ACKNOWLEDGMENTS

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