MINI REVIEW

Monitoring behavior: assessing population status with rapid behavioral assessment

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Abstract

Despite years of effort from behavioral ecologists, animal behavior has not been fully integrated into the field of conservation biology. We propose a novel framework to join these fields through the use of demographic models. We present three strategies for incorporating behavior in demographic models, outline the costs of each strategy through decision analysis, and build on previous work in behavioral ecology and demography. We then provide practical recommendations for applying this framework to management programs. First, relevant behavioral mechanisms should be included in demographic models used for conservation decision making. Second, rapid behavioral assessment is a useful tool to approximate demographic parameters through regression of demographic phenomena on observations of related behaviors. Behaviorally estimated parameters may be included in population viability analysis for use in management. Finally, behavioral indices can be used as indicators of population trends. Rapid behavioral assessment holds promise as a cost-effective tool, but also represents a cost to model accuracy. We provide a framework for implementing rapid behavioral assessment through case studies of reproductive, foraging, and antipredator behaviors. We use a decision-theoretic approach to provide quantitative rules for identifying when metrics of animal behavior may be more meaningful than traditional population assessment.

Introduction

Despite more than a decade of research on conservation behavior (Clemmons & Buchholz 1997; Caro 1998, 1999; Gosling & Sutherland 2000; Festa-Bianchet & Apollonio 2003; Blumstein & Fernández-Juricic 2010), Caro (2007) conceded that there are no overarching theories to connect the two fields of behavioral ecology and conservation biology (but see Moore *et al.* 2008; Berger-Tal *et al.* 2011). Here we challenge this claim by providing a framework that relies on demography to integrate behavioral knowledge with quantitative conservation biology. This framework accommodates existing studies in the area of conservation behavior and indicates areas of future exploration.

The relationship between a population's demography and the behavior of its members is the basis of our conceptual framework (Figure 1). The interactions between behavior and population dynamics can provide structure to conservation programs through demographic models used in population viability analysis (PVA) in three ways: (1) including behavioral mechanisms that increase biological realism; (2) approximating demographic parameters through rapid assessment of behavioral indices; and (3) monitoring for behavioral warning signs of population decline. We use a decision framework based on these strategies to provide a quantitative method to assess the tradeoff between predictive ability and program cost. This combination of PVA, rapid assessment and decision analysis will provide logical guidelines in applications of behavior to management decisions.

Below we describe our three strategies for applying knowledge of animal behavior to demography through PVA. Management implications from these three

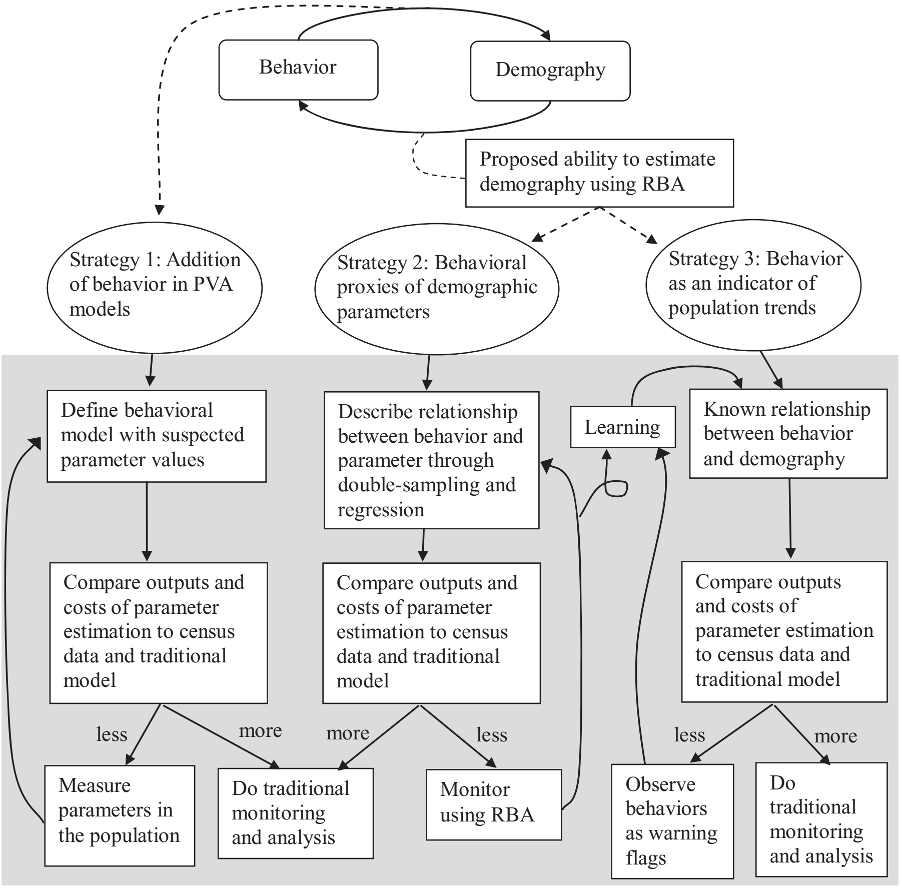


Figure 1 Schematic of the connection between behavior and demography, and three strategies to apply animal behavior to conservation programs. Each strategy involves measurement of model parameters either through traditional means or through rapid behavioral assessment and comparison of model outputs with traditional methods and census data. Our approach allows for continued updating of accuracy and precision through adaptive management (highlighted in grey) when costs resulting from each strategy are less than traditional monitoring. Implications from this framework are found in Table 1.

strategies are interpreted in a cost analysis to suggest when each strategy might be appropriate. We then detail the process of rapid assessment of behavioral indices as a means to estimate demographic parameters followed by examples of possible applications to three areas of conservation behavior concern: foraging, reproduction, and predator avoidance.

A framework for integrating animal behavior into conservation decision making

Models of population dynamics have been used extensively to make informed conservation decisions in the past (Mace & Lande 1991; Beissinger & Westphal 1998; Beissinger & McCullough 2002; Morris *et al.* 2002) and have become a critical aspect of successful conservation policy (e.g., potential biological removal in Marine Mammal Protection Act, the revised management procedure under the International Whaling Commission, and listing under the International Union for Conservation of Nature Red List and Endangered Species Act). Demographic models are also suitable tools for describing the feedbacks that may occur between demography and behavior (Figure 1). First, behavior of individuals can influence demography. For example, male dunnocks (*Prunella modularis*) tend to dominate winter food patches to the detriment of females (Davies 1992). These hierarchies can result in increased rates of female mortality, causing male-biased sex ratios following severe winters (Davies 1992). Demography may also influence the behavior of individuals, as can be seen in the harem-building saiga antelope (*Saiga tatarica*). When sex ratios are more balanced, males compete for access to harems of females. As a result of intense hunting of male antelope for their horns, some remaining populations have been shifted to extremely female-biased sex ratios. This rarity of male saiga has caused a switch in mating behavior: now dominant females restrict access to rare males (Milner-Gulland *et al.* 2003). This change in behavior may be a source of positive density dependence (i.e., Allee effect, Stephens & Sutherland 1999) in these populations, reducing the fecundity of subordinate females that are not able to mate and bear offspring.

Managers and conservation biologists can make use of the links between behavior and demography by including them in their predictive models or by using behaviors as indicators of demographic parameters and population trends (Figure 1). Here we describe three strategies for incorporating behavior into population monitoring programs. Each has implications for population viability; we interpret the implications of these modeling consequences on management by means of a cost analysis (Box 1).

Box 1: Formulation of the behavioral monitoring decision analysis.

Our decision analysis results from an extension of the cost equation described by Field *et al.* (2004):

$$C_m = M_m + x[p_m A + (1 - p_m)L] + (1 - x)\alpha_m A$$

Here the total program cost (C) is the sum of the cost of a monitoring program (M_m) using strategy m, mitigation actions (A), and the loss (L) associated with a change in the population's status. These mitigation and loss costs are modified by the probability of the true population state (x), the power (p_m) of the monitoring program to detect a change in this state, and the probability of false detection of a state change (α_m), or the Type I error rate. In their application, Field *et al.* (2004) define x as the probability that the rate of site occupancy has decreased significantly (determined by α) during a given time interval. Instead, we describe x as the probability that the population is displaying a growth rate more extreme than some threshold value, beyond which mitigation action is necessary. This interpretation can be applied to other conservation metrics, such as a probability of quasi-extinction or heterozygosity in the population. Calculating the power of each strategy will vary based on the strategy and the method of monitoring used. Costs of behavioral strategies (C_B) can be compared to those incurred through traditional monitoring methods (C_T).

Because the benefit of reduced monitoring costs depends in part on the ability of a model to predict population dynamics, our framework assumes that some amount of population data exist for comparison to model predictions. If no census data are available, it would likely be best to monitor using traditional methods, though there may be more cost effective options (see McDonald-Madden *et al.* 2010). In cases where future censuses are planned in conjunction with one of the monitoring strategies, the likelihood of the true population state and the power of each model can be updated as in an adaptive management context. Under an adaptive management scheme using Bayesian updating, more precise estimates of population growth may be obtainable rather than estimation of growth rates beyond a threshold. This cost analysis framework can also be expanded to incorporate various uncertainties in observation and process error in x (see Williams *et al.* 2002; Field *et al.* 2005).

Strategy 1: including behavior in PVA models

Much attention has been given to describing the inclusion of behavioral phenomena in population models (Sutherland 1996; Hastings 1997; Ebert 1999; Caswell 2001; Morris & Doak 2002). This strategy is already displayed in spatially explicit population models that incorporate dispersal behavior (e.g., González-Suárez & Gerber 2008; Revilla & Wiegand 2008). In addition, when mating behavior is included in population models, it can result in more accurate estimates of population growth rates (Gerber 2006), which may then better inform management decisions and harvest protocols (Horev *et al.* 2012). Greene *et al.* (1998) have shown that incorporating mating system and paternal care in population models can elucidate the risks of directed harvests in African game animals. The drawback to these additions, however, is that they result in more complicated models, which in turn often leads to increased cost due to the need for parameter estimation (e.g., increased radio tagging of individuals to describe movement behavior or DNA testing for paternity analysis). Additionally, it should also be noted that more complex models do not necessarily perform better in a predictive sense than simpler models because estimation uncertainty increases with model dimensionality (Chatfield 1995; Friedman 1997). There is thus a tradeoff between the costs of monitoring through PVA and the accuracy of the model used. This tradeoff may be best explored within the structure of decision analysis (Box 1; Table 1).

If including behaviors explicitly in models results in more accurate descriptions of population dynamics in a threatened system, the benefit to wildlife managers and policy makers may be greater than the extra costs and effort required to create these new models. From a decision-theoretic perspective, including behavioral mechanisms in PVA models likely increases cost (M_1) and reduces model precision. However, if the behaviors prove to be crucial for understanding population dynamics, the power (p_1) of models using Strategy 1 will have increased accuracy in estimating population trends. In other words, if the increased complexity and cost of parameter estimation results in a more accurate estimate of population decline and its consequences, Strategy 1 should be considered.

Strategy 2: behavioral observation as a proxy for demographic parameters

It may be possible for conservation biologists to estimate latent demographic rates through observation of certain

Table 1 Consequences of Strategies 1, 2, and 3 on population viability models and program costs as compared to those of the traditional monitoring technique (T)

	Strategy 1: addition of behavior in PVA models	Strategy 2: behavioral proxies of demographic parameters	Strategy 3: behavior as an indicator of population trends
Complexity of resulting model	Increased	No change	Decreased
Expected accuracy	Increased	Decreased	Decreased
Cost	Increased $(M_T < M_1)$	Decreased $(M_T > M_2)$	Decreased $(M_T > M_3)$

behaviors (Figure 1). The simplest models of population dynamics describe how birth (*b*) and death rates (*d*) interact to result in populations that change over time. By observing particular behaviors that are known to be correlated with demographic rates, researchers can uncover the parameters underlying the dynamics of monitored populations. Wildlife managers should be able to observe behaviors related to birth (e.g., nursing or parental care) and survival (e.g., foraging efficiency or predator wariness) and use them as proxies of the true rates (*b* and *d*, respectively).

Box 2: Rapid behavioral assessment applied to California sea lions.

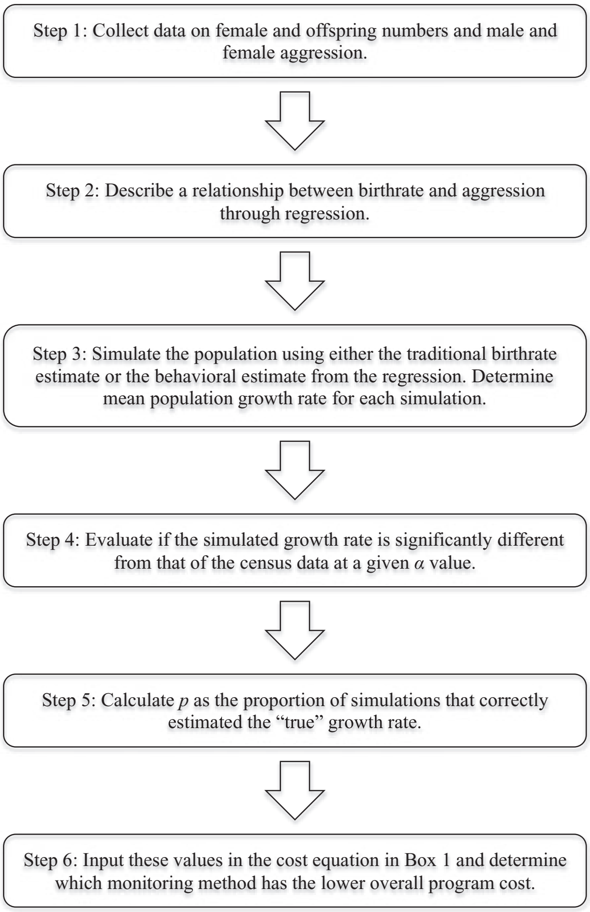
Here we provide an applied example of RBA monitoring of California sea lions with each step summarized in Figure 2. In their study in the Gulf of California, Mexico, Gerber *et al.* (2010) observed behaviors of California sea lions at breeding colonies and related these behaviors to the female reproductive rate, measured as the ratio of average number of pups to females observed at the height of the breeding season. They found that male and female aggression rates and male territory size are moderate predictors ($R^2 = 0.254$) of reproductive rate at these colonies. Using the regression described in their study (see the Appendix for details), we modeled the population dynamics of the breeding colony that occurs on Los Islotes island in the Gulf of California, Mexico. We employed both the birthrate estimated by count data (Demographic model) and that from the RBA regression (RBA model) in Gerber *et al.* (2010) to project female abundance through 28 years of census data.

We evaluated the cost of monitoring to detect the "true" mean growth rate, as defined by diffusion approximation of the census data, at a significance level of $\alpha = 0.05$. We found that the probability that the true mean growth rate is below our threshold is $x = \Pr(\mu < 0) = 0.102$. The Demographic model using empirical estimates of birthrate detected this true growth rate with a power of $p_T = 0.868$, while the RBA model had a power of $p_B = 0.679$. The cost of making five repeated observations over 28 years for parameter estimation was $M_T = \$428$ for traditional sampling and $M_B = \$129$ for RBA sampling. With these costs, monitoring through RBA is recommended for each level of mitigation cost (*A*) investigated for costs of population loss (*L*) less than \$20,000 (one colony). For example, when mitigation costs are $A = \$5000$ and loss from declining populations amount to $L = \$10{,}000$, total expected costs are $C_T = \$1228$ and $C_B = \$1025$ for traditional and behavioral monitoring, respectively. However, when costs related to declining populations are $L = \$50{,}000$, RBA monitoring is not advised ($C_T = \$1764$ and $C_B = \$2330$). This result is influenced by the bias of the RBA model, which in our case predicts lower growth rates than the Demographic model, but this may be a benefit in monitoring for conservation purposes. As Field *et al.* (2004) discuss, in many cases it may be better to assume that a monitored population is in decline and choose the monitoring strategy that allows you to detect this trend cost-effectively. We therefore remind practitioners to investigate the biases of their models before making final management decisions.

Instead of increasing costs through model complexity, Strategy 2 may simply reduce the current cost of monitoring the population of concern (see Box 2). However, these strategies introduce greater errors in population trajectories due to variance in the correlation between the behavioral indicator and the true parameter (Table 1). Aside from process stochasticity, this noise in the correlation also includes the effects of factors such as population size, density, or environmental conditions that may affect this relationship. As long as this observation error is small in relation to the benefits incurred from reduced costs in making these parameter estimations (M_2), Strategy 2 may be an important monitoring option. Under our decision analysis scheme, decreases in M_2 may outweigh increased error rates (α_2 and $1 - p_2$). If the combination of estimates from Strategy 2 and their reduced costs still result in adequate detection of population trends, management programs may be able to save resources through implementation of this strategy. By approximating demographic rates in this way, managers could then allocate resources to other crucial aspects of species conservation.

Strategy 3: behavior as an indicator of population trends

In well-studied systems, we may detect a relationship between certain behaviors and population trend metrics such as population size, density, or growth. These relationships could then be used as rules of thumb to describe qualitative patterns of population status or trends. In this case, changes in population size or composition may result in a marked switch from one behavior to another. Observing these behavioral changes would allow managers to anticipate the fate of populations and



Step 1: Collect data on female and offspring numbers and male and female aggression.

Step 2: Describe a relationship between birthrate and aggression through regression.

Step 3: Simulate the population using either the traditional birthrate estimate or the behavioral estimate from the regression. Determine mean population growth rate for each simulation.

Step 4: Evaluate if the simulated growth rate is significantly different from that of the census data at a given α value.

Step 5: Calculate p as the proportion of simulations that correctly estimated the "true" growth rate.

Step 6: Input these values in the cost equation in Box 1 and determine which monitoring method has the lower overall program cost.

Figure 2 Summary of methods for evaluating rapid behavioral assessment of a breeding colony of California sea lions.

impose management decisions based on early behavioral warnings. This process would only be acceptable in areas where behavioral observation and management are well established and the interaction between behavior and population dynamics is well understood. In the case of saiga harvesting outlined above, because viable populations of saiga have been shown to depend on the proportion of adult males (Milner-Gulland 1994, 1997), sustainable harvest of males may be restricted to years when guarding of males is not observed.

Although this strategy is understandably less accurate than detailed monitoring, it might act as an inexpensive warning flag for wildlife managers (Table 1). In our decision analysis, Strategy 3 would inflate the variance around model predictions, reducing power, though the costs (M_3 and possibly A) may be reduced if an appropriate indicator is found and if mitigation costs are lowered by taking early preventative action.

Rapid behavioral assessment

Before Strategies 2 or 3 can be implemented, a clear relationship must be drawn between a behavior and a related demographic phenomenon. Rapid assessment techniques can provide a means to define this relationship by observing the behavioral indices and estimating demographic parameters. Rapid behavioral assessment (RBA), typified by an intensive initial double-sampling (Eberhardt & Simmons 1987) of both the targeted behavior and demographic data followed by continued monitoring of the behavioral index, may provide the data needed to implement Strategies 2 and 3 above (Figure 1). A study of the chough (*Pyrrhocorax pyrrhocorax*) by Kerbiriou *et al.* (2009) is a helpful example of using RBA for estimating juvenile survival. During their study the researchers observed the spatial distribution and foraging behavior of choughs on Ouessant island in France and monitored monthly survival of juveniles color-banded as fledglings. They found that foraging frequency and juvenile survival were both negatively correlated with tourist visitation (Kerbiriou *et al.* 2009). Kerbiriou *et al.* (2009) argue that this reduction in survival is due to the observed decrease in foraging resulting from human disturbance after fledging. Because data on both foraging behavior and juvenile survival were collected for this population, a clear association could be derived from regression models to describe juvenile chough survival as a function of their foraging habits.

Kerbiriou *et al.* (2009) applied their findings to an individual-based population model and found that the prospective increase in tourism on the island increased the short-term extinction probability of this population due to the adverse effects of disturbance on foraging and the resulting decrease in juvenile survival. Similar population models can be constructed using the regression between this behavior and the demographic parameter to estimate population trends. Models using both the behavioral estimate of the demographic parameter and the traditional parameter estimate can be compared to quantify the departure of the RBA model from the traditional demographic model (i.e., estimate the power of the RBA model, p_B, and the traditional model, p_T). Multiple methods of model comparison including information criterion techniques, comparison of resulting growth rates, probabilities of extinction, and absolute differences in estimated population sizes resulting from each model should be used to determine the accuracy of the model that employs RBA beyond the power analysis described in Box 1. To the extent that error in the behavioral estimate results from small sample sizes, the lowered costs from RBA may allow for larger samples, resulting in lower measurement error. We provide a full example of the RBA process with a worked decision analysis for monitoring California sea lion populations in Box 2.

We do not expect that this method of parameter estimation will be appropriate for all demographic parameters as some parameters are more sensitive to errors in estimation than others. Therefore, we suggest that RBA may be most useful for estimating parameters with low to moderate model sensitivities. This is because error introduced through regression will become magnified in highly sensitive parameters, but for parameters with little sensitivity there is no need for such detailed estimates.

Because many studies have described systems where Strategy 1 is important for conservation, we focus the remainder of our review on examples of Strategies 2 and 3. Specifically, we characterize three areas of vertebrate animal behavior that greatly influence the viability of populations: reproduction, foraging, and antipredator behaviors. Within each section we provide case studies of systems amenable to Strategy 2 or 3 and where RBA may prove to be a useful monitoring technique. We acknowledge that these examples stem from studies of birds and mammals, but are confident that the basic relationships between behavior and demography permeate through a broad scope of animal taxa, including arthropods, reptiles, and even mollusks (Payne *et al.* 2011).

Reproductive behavior

The behaviors surrounding reproduction, parturition, and parental care are closely related to rates of reproduction and offspring survival. In particular, behaviors stemming from the mating system may have implications for female fecundity and ultimately population growth rates (Gerber 2006). It has also been proposed that small populations, which typically have high conservation priority, may be limited by male fecundity as well as that of females (Gerber 2006; Rankin & Kokko 2007). The demographic rates surrounding reproduction may therefore be approximated through observations of reproductive behaviors, especially in systems where these rates and their associated behaviors vary between different life stages or sexes (as detailed in Box 2).

Strategy 2—In a long-term study of bearded vultures (*Gypaetus barbatus*) in the Spanish Pyrenees, Carrete *et al.* (2006b) correlated the occurrence of polyandrous breeding nests with habitat saturation. They found that as the population of bearded vultures grew and traditional monogamous breeding pairs claimed available territories, breeding trios composed of one dominant male, one subordinate male and a female began to be established in older, more productive breeding territories. This change from monogamous to polyandrous nests was also highly correlated with a reduction of fecundity per nest in these traditionally productive breeding pairs, which reduced the productivity of the population as a whole (Carrete *et al.* 2006b). In this system, where the relationship between polyandrous nests and nest productivity is known, RBA of nest mating systems may prove useful in estimating fecundity of the population. It may be possible to assess population viability or carrying capacity from these estimates for future management action.

Strategy 3—To further the example of the bearded vulture (Carrete *et al.* 2006b), the onset of polyandry may be an indicator of a demographically robust population where all available habitat has been filled through increasing vulture abundance. In contrast, if this habitat saturation is facilitated by supplementary feeding by wildlife managers, which may reduce dispersal of young vultures, a switch to polyandry near these supplementary feeding points may serve as a signal to stop supplementary feeding to encourage dispersal (Carrete *et al.* 2006a). In systems such as this and the saiga antelope from the example above, shifts in mating strategy defined through previous studies (Strategy 2) may serve as thresholds for wildlife management and policy.

Foraging behavior

Optimal foraging theory indicates that in a predictable environment there is generally one optimal foraging pattern (Pyke *et al.* 1977), which is manifest in the role and distribution of individuals within a population. As the environment becomes less predictable due to a number of pressures, foraging patterns tend to change. These environmental pressures can be biotic in origin and include small population densities of threatened species (Reed 1999), a reduction in important cues that may indicate high patch quality (Reed 1999), increased predation risk (Heithaus *et al.* 2007), or poaching (Donadio & Buskirk 2006) to name a few. Abiotic pressures (e.g., temperature, nutrient content, or amount of cover) may also result in changing foraging patterns. Often these environmental pressures combine in tradeoffs between foraging and other vital processes, such as reproduction or evading predation. Because these optimal foraging behaviors are a function of the complex interaction between biotic and abiotic pressures, managers may be able to gain insight into a population's vital rates through behavioral observation in conjunction with simple abiotic measurements. Sutherland (1996) provides detailed explanations and applications of foraging theories in population models.

Strategy 2—The pressures, or costs, surrounding foraging are threefold: energetic costs (E), the cost of predation (P), and the cost of missed opportunity (M), and are directly related to harvest rate (H) by the equation: $H = E + P + M$ (Morris *et al.* 2009). The density of food in a patch at which harvest rate satisfies this equality is the giving-up density (GUD, Brown 1988). From this equation we see that as risk of predation while foraging in the patch increases, so does the GUD (Olsson & Molokwu 2007). Alternatively, in food-scarce habitats, the GUD of a patch will likely be lower (Olsson and Molokwu 2007) because of the heightened energetic requirements of the foraging individuals. By presenting animals in a population with experimental patches, the foraging animals provide information about the level of environmental pressure in their habitat.

Olsson *et al.* (1999) applied this sampling technique in a population of threatened lesser spotted woodpecker (*Dendrocopos minor*) and found that average GUDs were correlated with individual reproductive success. They showed that individual woodpeckers that left foraging patches with lower densities of wood-inhabiting insect larvae also initiated egg-laying later than those that left patches at higher prey densities (Olsson *et al.* 1999). High levels of GUD were also significantly associated with higher rates of offspring fledging that year. The researchers conclude that individual GUDs may be an indicator of individual reproductive success. Importantly, these GUDs were observed weeks to months before the onset of breeding in the spring. By monitoring for reduced GUDs in this population late in the winter, managers may be able to anticipate and mitigate depressed reproductive output later that year through supplemental feeding.

Strategy 3—Many studies have been conducted to describe the optimal feeding patterns involved in domestic animal husbandry. These optimal patterns have been linked to reproductive success and fawn survival in domestic sheep (McEvoy & Robinson 2002). McEvoy and Robinson (2002) describe that variation between foraging extremes, or a stuff-starve foraging pattern, during pregnancy may lead to lower embryo survival, reducing reproductive output. Nutritional content of forage during gestation is also crucial for offspring survival and may compromise ovary development in unborn females (Yakovleva *et al.* 1997; Nazarova & Evsikov 2008). Similar or more pronounced patterns are likely to appear in avian and reptile taxa, as they must provision offspring with all required nutrients before egg-laying (Martínez-Padilla 2006; Nelson *et al.* 2010). In birds, these behaviors may be used to monitor fledging success of breeding pairs. Mariette *et al.* (2011) found that visitation rates at local feeders by zebra finches (*Taeniopygia guttata*) predicted crop contents in nestlings—a possible indication of nestling fledging and reproductive success of the parental pair. Monitoring foraging frequency and choice of forage preceding and during the breeding season of a target species may allow managers to recognize the possibility of compromised reproduction or offspring survival due to malnutrition before the effects are observed in the following year(s).

Antipredator behavior

Antipredator behaviors, such as flight response and vigilance, often reflect an animal's previous exposure to predation. Therefore, animals experiencing these dangerous situations should be more wary of their surroundings compared to naive individuals. Observing and quantifying these fear behaviors through rapid assessment may in some cases give conservation personnel a more accurate measure of the level of experience a focal population has with predation. Although these behaviors are termed "antipredator" behavior, in many cases these behaviors are displayed in response to human-induced threats.

Strategy 2—To estimate the amount of experience animals had with human contact, Caro (2005) recorded the reaction of African mammals to the presence of his vehicle inside and outside of the protected Katavi National Park. He found that many species became more wary or fled from the vehicle more often outside of the park—where hunting pressure is known to be higher—than inside its boundaries. Donadio and Buskirk (2006) apply this hypothesis further, suggesting that flight response may serve as an indicator of poaching pressure. They recorded the distance and frequency that groups of guanacos (*Lama guanicoe*) and vicuñas (*Vicugna vicugna*) fled from researchers standing in the bed of a truck driving past the heard. They found that the animals fled more frequently in areas suspected of higher poaching rates due to less protection from law enforcement (Donadio & Buskirk 2006).

Surveying these flight behaviors through rapid assessment may provide estimates of survival probability in these herds. Also, if estimates of both legal hunting and poaching pressures exist, managers may be able to model the effect of poaching on population persistence. These estimates can then be integrated into PVA models to direct management decisions on antipoaching policies.

Strategy 3—Human-induced stresses may not always come in the dramatic form of poaching. In a world of increasing ecotourism, some conservation biologists have started to question the effect of human disturbance in visited populations (Frid & Dill 2002; Blumstein & Fernández-Juricic 2010). Similar to the chough in the example above, European shag (*Phalacrocorax aristotelis*) are costal breeding sea birds that are threatened by disturbance to foraging juveniles (Velando & Munilla 2011).

Table 2 Implications of animal behavior for population demography and population viability analysis, including behavioral data that can be collected to estimate PVA parameters

Behavior	Implication for PVA	Data collection	References
Reproduction			
Mating system	Fecundity Sex ratio Patch choice Genetic diversity	Type, # of mates, mating rates, location, time, frequency	Shuster & Wade 2003; Carrete *et al.* 2006b; Gascoigne *et al.* 2009; Jenouvrier *et al.* 2010
Mate choice, mate competition, Mate guarding	Genetic diversity Fecundity Cost: energetic and predation pressure	Paternity, cryptic choice, which mates are selected, # of fights/displays, # of successful matings, time spent guarding, # of mates	Cooper & Vitt 2002; Matsubara 2003; Clutton-Brock 2007, 2009
Dispersal	Immigration/emigration Genetic diversity, inbreeding Cost: risk of dispersal	Rate, survival, which populations to/from	Peacock & Smith 1997; Sterck *et al.* 2005; Randall *et al.* 2007; Robbins *et al.* 2009
Parenting	Fecundity, mating success	Duration, effort, success	Trivers & Willard 1973; Jennions & Polakow 2001
Foraging			
Diet choice	Survival: Prey availability Cost: New predation pressures, infection risk	Forage type, nutrient quality	Coolen *et al.* 2007; Heithaus *et al.* 2008
Patch choice	Immigration/emigration	Type of patches, rate of movement, length of stay	Sutherland 1996; Heithaus *et al.* 2007; Kerbiriou *et al.* 2009
Rate/Time	Cost: Predation pressures, nutrient values Carrying capacity	When, how often, and how much	Sutherland 1996; Morris & Mukherjee 2007; Mariette *et al.* 2011; Oppel *et al.* 2011
Missed opportunity	Survival: Food availability Cost: Predation pressure	Giving-up density	Whelan & Jedlicka 2007; Morris *et al.* 2009
Anti-Predator			
Flight	Cost: Poaching, predator avoidance Survival	Distance from predator, time before flight	Caro 2005; Donadio & Buskirk 2006
Predator inspection, detection and vigilance	Cost: Re/introduced predator species Survival Growth rate Group size	Distance, how inspection happens, who inspects, inspection/detection rate, size of group, who keeps watch, accuracy	Manor & Saltz 2003; Mooring *et al.* 2004
Generalization and Discrimination	Cost: Re/introduction of predators Survival	Rate of learning, accuracy	Griffin *et al.* 2000; Coleman *et al.* 2008; McCleery 2009
Disturbance	Cost: missed opportunity Survival	Distance, recovery, types of disturbance	Manor & Saltz 2003; Blumstein *et al.* 2005; Velando & Munilla 2011

Velando and Munilla (2011) show that foraging European shag at the Cíes islands in Galicia, Spain are highly disturbed by the presence of boats in important foraging patches. They found that the birds group closer together and reduce foraging dives drastically as the number of boats increases (Velando & Munilla 2011). By monitoring foraging patches for dense groupings of European shag, action may be taken to reduce disturbance levels and therefore mitigate future loss of juvenile birds. Observation of disturbance behaviors such as this and their effects on population growth may prove important in guiding management programs and policy in these tourism destinations.

Management applications

We provide a conceptual framework that is rooted in previous studies of animal behavior and population dynamics to provide structure for applying behavioral studies to conservation decision making. We have outlined three strategies to aid conservation biologists in integrating this knowledge into their management programs with emphasis on the areas of reproductive, foraging, and antipredator behaviors. In particular, Strategy 1 incorporates behaviors explicitly into demographic models. Strategy 2 assumes that behaviors and demographic parameters are correlated and makes use of this relationship to estimate the latter from the former through rapid behavioral assessment. Strategy 3 uses these behavioral indicators as warning flags against population decline. Because these three strategies, their associated models, and the actions they require can be combined into decision analysis, the above framework not only makes use of behavioral ecology theory, but also provides general rules for when incorporating behavior into management is beneficial.

Our framework and particularly the technique of RBA are methods that should lead to reduced costs over the course of a monitoring program. The examples of RBA provided above are only a small sample of the wealth of knowledge behavioral ecology theory has brought to the attention of behaviorists and conservationists alike. A more detailed list of behaviors and their conservation implications can be found in Table 2, though we do not intend for this list to be an exhaustive representation of these important relationships. Our approach is not intended to replace standard methods of population parameter estimation, as these will be more effective methods for population management in most situations. We recognize that such methods are essential for wildlife management and provide invaluable data for addressing population status and viability. We envision an adaptive management approach that incorporates RBA into monitoring procedures in conjunction with traditional demographic parameter estimation. In this context, this work encourages managers to consider RBA as one of the possible standard tools for demographic parameter estimation that should be used when it is the most efficient option among the possible parameter estimation methods. This demographic framework to incorporate behavior into conservation decision making may be broadly used in policy and management. Integrating behavioral and population dynamic information with decreased program costs may ultimately improve the efficacy of conservation actions.

Appendix: Methods for worked example in California sea lions

We model the breeding population of California sea lions on the island of Los Islotes, Gulf of California, Mexico using a stage-structured matrix model with two sources of birthrate estimates: (1) demographic estimates calculated as the ratio of mean pups to mean females observed, and (2) estimates resulting from imputing behavioral observations of adult sea lions into a regression described in Gerber *et al.* (2010; see Wildermuth *et al.* (in prep.) for further details and analysis). The model reflects the female portion of the population in three stages: pups (P) < 1 year., juveniles (J) from years 1–4, and adult females (F) ≥ 5 years:

$$\begin{aligned} P_{t+1} &= I \times B \times F_t \times SR \\ J_{t+1} &= S_P \times P_t + S_J \times J_t \\ F_{t+1} &= G \times J_t + S_F \times F_t \end{aligned} \tag{A.1}$$

$$I = \frac{1}{(1 + (N_t/K))}, \tag{A.2}$$

where N_t is the total population, and with the resulting process matrix:

$$\begin{bmatrix} 0 & 0 & I \times B \times SR \\ S_P & S_J & 0 \\ 0 & G & S_F \end{bmatrix}. \tag{A.3}$$

Here, S indicates survival of pups (S_P), juveniles (S_J), and females (S_F). Juveniles survive and mature at rate G to become adult females. Birthrate (B) describes the number of yearling pups per female averaged across the study population. Stochasticity was incorporated by selecting from previously published estimates of each parameter (survival rates $n = 4$, growth rate $n = 2$) or from birthrates observed by Gerber *et al.* from 2004 to 2007. New pups born each year are multiplied by an even female sex ratio ($SR = 0.5$), so that we only follow the female portion of the population. The I term (Equation A.2) reflects a form of logistic density dependence that discounts the overall pup birthrate as the total population size reaches and exceeds the carrying capacity parameter K (Dobson & Lyles 1989).

Because the carrying capacity parameter ultimately acts as a scalar of the combination of other parameters in the model, final maximum population size is highly dependent on the value chosen for K. For this reason we first found the best estimate of K for the model using a demographic estimate of birthrate because this model should reflect true population dynamics best (Beissinger & Westphal 1998; Morris & Doak 2002). The best K estimate was found by calculating the sum-of-square value (Hilborn & Mangel 1997) of each model to the census data from 1980 to 2008. We searched over a range of possible K values between 1 and 400 and summed across simulations within each candidate value of K. The value of K resulting in the smallest sum-of-square value is considered to be the best estimate of this parameter.

We compare outputs of the model run with a demographic estimate of birthrate (Demographic model) and a behaviorally approximated birthrate (RBA model). The demographic estimate consists of the four observed reproductive rates for 2004–2007 reported in the supplementary material of Gerber *et al.* (2010). The RBA estimate used female and male aggression rates observed at Los Islotes in these four years as input for their regression describing birthrate from these behaviors:

$$B = 1.178 + 0.044 \times A_{\mathrm{F}} - 0.177 \times A_{\mathrm{M}}. \qquad \text{(A.4)}$$

Here, birthrate (B) increases with increasing female aggression (A_{F}), likely due to females protecting their young pups from others. In contrast, birthrate is negatively correlated with male aggression (A_{M}), which is likely due to increased risk to pups from highly territorial males. Because the RBA estimate of birthrate incorporates two different yet possibly correlated behaviors, we restrict the model to select both behaviors from the same year (i.e., male and female aggression from 2005 are always used in Equation A.4 at the same time).

All demographic parameters were randomly selected with replacement in each year of the model and placed into the process matrix to project the population into the next year. Each model was initiated with the abundances of each stage observed in 1980 and simulated 20,000 times.

Using diffusion approximation (Dennis *et al.* 1991), we estimated the mean and standard error of growth rate from census data. With these estimates, we described the distribution of the mean census growth rates and integrated the probability distribution function over all growth rates below $\mu = 0$ and set this value equal to x. The same procedure was performed for simulated data from the RBA and demographic models to determine the upper and lower confidence intervals of individual simulations. The Type II error rate (β) was calculated as the frequency of simulations that did not contain the mean of the census data within their 95% two-tailed confidence intervals ($\alpha = 0.05$). Power was calculated as $p_m = 1 - \beta$.

Monitoring costs were estimated from person-hours required for making birthrate estimates at the standard U.S. federal employee GS-5 pay rate in 2005. We analyzed the cost equation from Box 1 for a range of action and loss costs between \$100 and \$5 million, assuming that monitoring, action, and loss costs increase with biological consequences (i.e., $M_{\mathrm{m}} < A < L$).

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