

Anthropogenic influences on natural animal mating systems

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Anthropogenic influences on the natural world are widespread and well studied from various ecological vantage points. Their behavioural implications, however, are comparatively less well understood. We review four categories of influence on natural animal mating systems: habitat fragmentation, climate change, pollution and selective harvesting. We adopt a predictive approach, first reviewing the ecological determinants of mating system variation and then investigating how these determinants may be affected. Habitat fragmentation and climate change are directly altering the two fundamental predictors of mating system variation: the spatial and temporal distributions of resources. Pollution has implications for mating systems, via, for example, feminizing effects of endocrine disruptors and impeded efficacy of sexual communication. The influences of selective harvesting arise from the removal of phenotypic (and in some cases, genetic) variation in sexually selected traits. The ecological (e.g. by serving as an underlying mechanism contributing to Allee effects) and evolutionary (e.g. by driving microevolutionary trajectories that run counter to sexual selection) consequences of mating system disruption may be severe. The current lack of data, however, makes rigorous assessment of these consequences premature. Nevertheless, there is an analytical framework that can be used to make quantitative predictions, and we argue that applying it more broadly will help improve our understanding of the causes and consequences of anthropogenic influences on natural animal mating systems. © 2011 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Anthropogenic influences on the natural world are now ubiquitous. Resource extraction and development have led to habitat fragmentation (Saunders et al. 1991; Andr n 1994). Climate change has altered the phenologies and distributions of populations (Parmesan 2006). Pollution has had myriad detrimental effects on the health of organisms (Carson 1962; Weilgart 2007) and harvesting has negatively influenced the viability of populations (Myers et al. 1995). These implications are intensively studied within the fields of population, community and spatial ecology and are the subjects of a number of dedicated journals and textbooks (e.g. Pullin 2002; Moilanen et al. 2009). Within animal behaviour, however, they remain comparatively underappreciated (Sutherland 1998; Caro 2007). In this review, we address one area with potentially important ecological and evolutionary consequences: anthropogenic influences on the mating systems of natural animal populations.

Two patterns, consistent across diverse taxa, originally led Darwin (1871) to infer that sexual selection must be a potent evolutionary force. First, within species, males and females often display striking divergence in traits associated with reproduction. Second, the males of closely related species often show marked character displacement in these same traits. In the decades following Darwin's articulation of sexual selection, both theoretical and empirical treatments have supported his original assertion of its efficacy (Andersson 1994 and references therein). It is now acknowledged that understanding patterns of biological diversity requires an appreciation of both natural and sexual selection, and understanding the action of sexual selection requires knowledge of mating systems.

Mating systems refer to the ways in which members of a population achieve reproductive success, including the number of mates acquired by individuals, the behavioural strategies used in acquiring these mates, and any patterns of parental care (Emlen & Oring 1977). Females, by definition, produce relatively few, well-provisioned, gametes (Parker et al. 1972; Bell 1978). Reproductive success of females is thus assumed to be limited by the resources that can be allocated to reproduction, and the spatial and temporal distributions of resources in the environment are hypothesized as the primary predictors of the distributions of receptive females (Bateman 1948; Trivers 1972; Emlen & Oring 1977). Males, by

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contrast, produce a vast number of comparatively inexpensive gametes, and male reproductive success is thus assumed limited by the acquisition of mates (Bateman 1948; Trivers 1972). Because of this unequal investment in reproduction, the relative availability of reproductive males and females differs. Consequently, the limited sex (typically males) competes for the limiting sex (typically females) (Clutton-Brock & Vincent 1991; but see Kokko & Jennions 2008 for a criticism of conventional sex role theory), and the distribution of receptive females creates the landscape of sexual selection for males.

Anthropogenic influences often act directly on the predictors of mating system variation. Habitat fragmentation alters the spatial distributions of resources, and the most often recorded ecological responses to climate change are shifts in the phenologies (i.e. temporal distributions of key life history events) of wild populations (Parmesan 2006). Pollution affects the reproductive behaviour of individuals (e.g. following exposure to endocrine disruptors; e.g. Colborn et al. 1993) and the efficacy of sexual signals (e.g. Lurling & Scheffer 2007). Finally, selective harvesting removes phenotypic (and in some cases, genetic) variation in sexually selected traits (Coltman et al. 2003; Olsen et al. 2004).

Our objective, rather than exhaustively cataloguing the documented effects, is to adopt a predictive approach, first reviewing the biological parameters underlying natural mating system variation and then investigating the ways in which these parameters have been altered by human activities. Theoretical (Emlen & Oring 1977) and analytical frameworks (Wade 1995; Shuster & Wade 2003) are currently available to examine these relationships. In some cases, empirical evidence has supported predictions based on these frameworks, while in others, predictions are more speculative. We argue, however, that forming a priori predictions of the impacts of human activities, rather than attempting a posteriori inference based on patterns arising from them, will allow for a more rigorous analysis of how these activities affect mating systems. In addition to providing insight into the mechanistic bases underlying conservation challenges (e.g. Allee effects; Allee 1931), we also suggest that exploiting the environmental variation arising from anthropogenic impacts provides new opportunities for fundamental research to improve our understanding of the influences shaping mating systems in nature.

A PREDICTIVE FRAMEWORK

The fundamental relationships between the spatial and temporal distributions of resources (and therefore, receptive females) and mating system variation allow for quantitative predictions as to how the latter may be affected by anthropogenic influence on the former. We refer readers to the original sources (Wade 1995; Shuster & Wade 2003) for a more detailed description and full derivation of the mathematical formulae but, briefly, the approach borrows Lloyd's (1967) ecological measure of density dependence (mean crowding) to quantify the spatial and temporal distributions of receptive females. The interaction of these distributions then predicts the opportunity for sexual selection on males (Crow 1958; Wade & Arnold 1980) and ultimately mating system variation.

The opportunity for selection sets an upper limit to the amount of adaptive change that selection may induce per generation and is equal to the total variance in reproductive success, divided by the square of the mean reproductive success (Crow 1958). In males (I_{males}), it is composed of both the variance owing to female reproductive success (I_{females}) and the variance in mating success among males (i.e. the opportunity for sexual selection (I_{mates}); Wade 1995). Consequently, with an equal sex ratio,

$$I_{\text{males}} = I_{\text{females}} + I_{\text{mates}} \quad (1)$$

and, therefore, the difference in sexual selection between males and females equals the opportunity for sexual selection in males, i.e.

$$I_{\text{mates}} = I_{\text{males}} - I_{\text{females}} \quad (2)$$

Although variation in I_{mates} can arise through random processes (Sutherland 1985), in general it is considered an important determinant of mating system variation (Wade 1979, 1995; Wade & Arnold 1980).

The spatial and temporal distributions of receptive females, represented as mean spatial and temporal crowding, respectively, are calculated based on their density in each of i habitat patches (Wade 1995) and across i time intervals (Shuster & Wade 2003), i.e.

$$m^* = \left\{ \sum m_i(m_i - 1) \right\} / \left\{ \sum m_i \right\} \quad (3)$$

$$t^* = \left\{ \sum t_i(t_i - 1) \right\} / \left\{ \sum t_i \right\} \quad (4)$$

where m_i and t_i , respectively, represent the number of females on the i th patch and in i th time interval. Equations (4) and (5) can be rewritten as

$$m^* = m + \{(V_m/m) - 1\} \quad (5)$$

$$t^* = t + \{(V_t/t) - 1\} \quad (6)$$

where m and V_m , respectively, represent the mean and variance in the density of receptive females per patch and t and V_t , respectively, represent the mean and variance in the number of receptive females over i intervals. If female density conforms to a Poisson distribution (i.e. $V_m/t = m/t$), m^*/t^* is equal to m/t .

The interaction of m^* and t^* predicts I_{mates} (Fig. 1; Shuster & Wade 2003). The two measures of mean crowding are analogous in that high values of each indicate clumped/synchronous receptivity, intermediate values indicate a random distribution, and low values reflect overdispersion. The consequences of each for mating system variation, however, are in direct opposition to one another. High values of m^* (i.e. spatially clumped females) elevate I_{mates} , while high values of t^* (i.e. synchronous reproduction) diminish it. In total, these relationships allow for an ecological classification of mating systems (Shuster & Wade 2003). For example, spatially clumped female distributions and asynchronous reproduction yield high values of m^* , low values of t^* , high values of I_{mates} and a predicted defence polygynous system (Fig. 1; Shuster & Wade 2003). Under these conditions, sexual selection should favour adaptations in males that allow them to defend multiple females or the resources upon which females rely (Clutton-Brock 1989). Moreover, these relationships are directly relevant to the anthropogenic influences on mating systems. For example, quantifying how altering resource distributions affects m^* and t^* allows for predictions of how I_{mates} , and ultimately, mating systems may respond, and I_{mates} provides a benchmark against which we can examine the strength of selection under selective-harvesting regimes.

HABITAT FRAGMENTATION

A combination of resource extraction and urbanization has drastically altered spatial resource distributions throughout the world (Saunders et al. 1991; Andr n 1994; Wiens et al. 2007), and the detrimental effects of these practices for population viability and ecosystem biodiversity are broadly acknowledged (Tilman et al. 1995; Henle et al. 2004). However, despite the potential for habitat

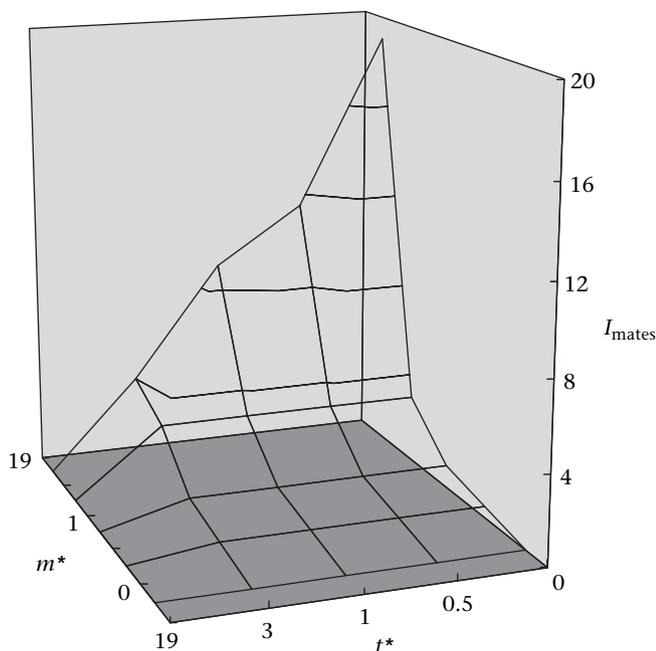


Figure 1. The relationship between the spatial (m^*) and temporal mean crowding (t^*) of receptive females and the opportunity for sexual selection in males (I_{mates}). m^* and t^* , respectively, quantify the spatial and temporal distributions of receptive females during the mating season. These resulting relationships can be used to predict mating system variation. For example, spatial clumping of females (elevated m^*) combined with asynchronous reproduction (diminished t^*) lead to high I_{mates} and selection favouring males' abilities to defend multiple females in female-defence mating systems. Data are from Shuster & Wade (2003) and the figure is redrawn from Figure 9.7 therein.

fragmentation to exert tremendous influence on natural mating systems and recent emphasis being put on such effects in plant systems (reviewed by Eckert et al. 2009), similar attention has not been paid to animal populations.

Theoretically, the pronounced habitat change wrought by anthropogenic influence provides powerful raw material with which to test Emlen & Oring's (1977) original hypothesis. Habitat fragmentation leads to spatially clumped resource distributions and, consequently, spatially clumped receptive females. Quantifying the variation in m^* resulting from this response then allows for specific predictions regarding mating system variation. Specifically, we would predict that spatially clumped resources will elevate m^* (equations (3) and (5); Fig. 1), increasing I_{mates} and potentially resulting in mating system transitions towards defence polygyny. Evidence of such a transition comes from a comparison of two neighbouring bobuck, *Trichosurus cunninghami*, populations. Whereas the mating system was socially monogamous in the more 'natural' forest habitat, a polygynous mating system prevailed in the fragmented roadside habitat (Martin & Martin 2007). Specific predictions in other species will require knowledge of the degree of habitat modification relative to the natural history of the species. In the Wellington tree weta, *Hemideina crassidens*, males attempt to defend harems of females that reside in tree cavities. The selective removal of older trees with large cavities will thus result in, on average, smaller harems and directly influence I_{mates} (Kelly 2008a). If fragmentation is severe and home range sizes of females are large, relative to the size of remnant fragments, the opposite scenario as that observed in bobucks may even be predicted. Specifically, if remnant fragments can only support single females, m^* , and consequently I_{mates} , will decrease (equations (3) and (5); Fig. 1) and a defence mating system would be predicted to shift to

scramble competition or even monogamy. Such a transition may have important consequences for population viability. If the ability to locate mates has not been strongly selected for in the traditionally defence mating system (sensu Lane et al. 2009), individuals may have difficulty finding mates, ultimately leading to declines in mean reproductive rate.

More generally, diminished levels of pairing success may result from low connectivity among habitat patches (Dale 2001). This result was observed in a population of Des Murs' wire tail, *Sylviothorhynchus desmursii* (Diaz et al. 2006) following fragmentation. However, similar results were not obtained from an American redstart population, *Setophaga ruticilla*, in which degree of forest cover did not predict levels of off-territory movement (Churchill & Hannon 2010). The extent to which mating systems are affected is thus likely to depend both on the severity of the fragmentation and the willingness of individuals to traverse inhospitable habitat.

Even if fragmentation does not influence behavioural pairing success, by impinging on individual movements, it may lead to decreased levels of multiple paternity. Elevated mean relatedness in remnant fragments is also likely to lead to concomitant increases in inbreeding. Both of these patterns have been observed in a population of agile antechinus, *Antechinus agilis*, following fragmentation of their native eucalypt habitat by commercial pine plantations (Banks et al. 2005). Effective kin recognition systems apparently prevented a similar increase in inbreeding in Cunningham's skinks, *Egernia cunninghami*, despite elevated genetic relatedness in remnant fragments (Stow & Sunnocks 2004). Unlike *A. agilis*, in which semelparity ensures that offspring will never encounter their parents (Braithwaite & Lee 1979), *E. cunninghami* form social groups consisting of a long-term monogamous pair and multiple generations of close kin. Selection has thus presumably favoured inbreeding avoidance mechanisms resulting from inherent kin recognition abilities. As a result, this population is less likely to suffer from inbreeding depression. It may be more vulnerable to reduced reproductive rates following severe fragmentation, however, should individuals refuse to mate with close relatives (as a result of so called 'glass effects'; Tainaka & Itoh 1996).

Reduced abilities to find mates and diminished dispersal are likely to influence natural populations in ways that extend well beyond their mating systems. Increased levels of inbreeding combined with reduced pairing success and gene dispersal are likely to exacerbate the initial effects of lost habitat and ultimately reduce the viability of populations (Banks et al. 2007). Mating system transitions are also likely to affect the fitness consequences of traits (Gwynne 1981), as well as the energetic (Lane et al. 2010) and life history (Roff 2002) costs of their maintenance. Ultimately, the landscape of sexual selection and even patterns of evolution may be affected. Importantly, the basic linkages between spatial resource distributions and mating system variation, when investigated within the analytical framework above, allow for a priori predictions that should be taken into account when assessing plans for habitat modification, rather than the a posteriori inferences based on resultant patterns.

CLIMATE CHANGE

The second ecological variable hypothesized by Emlen & Oring (1977) as a fundamental predictor of mating system variation, the temporal distribution of resources, has similarly been affected by anthropogenic influence. Widespread climate change over the past century has resulted in shifts in the phenology of many populations (Parmesan 2006). Documented effects include advances in the arrival and laying dates of migratory birds (Walther et al. 2002), emergence and parturition dates, respectively, of hibernating and euthermic mammals (Inouye et al. 2000; Réale et al. 2003),

spawning of anurans (Phillimore et al. 2010) and eclosure of insects (Robinet & Roques 2010).

Indirect evidence for mating-system-level effects of climate change comes from an interspecific analysis (García-Peña et al. 2009). Across shorebird species, migratory distance was negatively correlated with both the length of the reproductive season and ambient temperature on the breeding grounds. Presumably due to an energetic trade-off between the costs of long-distance migration and paternal care, males of species from more northern environments invested less in care of individual clutches and levels of polygyny were higher (García-Peña et al. 2009). The majority of climate-change models predict the most extreme levels of warming in the highest latitudes (IPCC 2007). García-Peña et al.'s (2009) results would thus predict that climate change should lead to shorter migration distances, longer breeding seasons, increased levels of biparental care and shifts towards monogamy in this clade.

Predictions about the influence of climate change on specific mating systems and patterns of sexual selection therein require an understanding of how t^* and sex-specific phenologies, respectively, may be affected. While estimates of these two variables are still relatively rare (but see Møller 2004; Rainio et al. 2007), there is a growing amount of information available from individual-based phenology studies. In many cases these data have been collected over multiple years or even decades (e.g. Réale et al. 2003; Charmantier et al. 2008) and, when analysed within the above framework, these data sets have the potential to provide unprecedented insight into temporal variation in mating system function as a consequence of climate change over multiple generations.

Variation in reproductive phenology may result from heritable genetic variance (e.g. Réale et al. 2003) and/or phenotypic plasticity (Przybylo et al. 2000). Heritable variation is clearly necessary for an evolutionary response to selection (Falconer & Mackay 1996), and both microevolution and plasticity may alter t^* . For example, more favourable conditions during avian migration may relax natural selection constraints on early arrival, thereby increasing the spread of arrival dates (diminishing t^* ; Morbey & Ydenberg 2001; Møller 2004). Under these conditions, polygynous mating systems are more likely to prevail following an increase in I_{mates} . However, determining optimal arrival dates also requires an understanding of the action of sexual selection (Kokko 1999; Morbey & Ydenberg 2001). Further complicating predictions is the potential for between-sex genetic correlations, such that evolutionary change in phenological traits in one sex is dependent on the magnitude of the genetic correlation with, and patterns of selection acting on, these traits in the other sex (sensu Kruuk et al. 2008). As for the heritability of phenological traits, therefore, these correlations will need to be quantified using appropriate pedigree information (e.g. Foerster et al. 2007).

Protandry refers to the earlier arrival of males, relative to females, in the breeding population (Morbey & Ydenberg 2001). It is typically interpreted in the context of the balance between natural and sexual selection, with sexual selection favouring an advanced phenology relative to natural selection (Kokko 1999). While most often studied in migratory birds, it has also been observed in hibernating mammals (Michener 1983), amphibians (Douglas 1979; Semlitsch 1985) and insects (Bulmer 1983). If climate change alters the balance between natural and sexual selection, it is conceivable that each sex will be affected differently. For instance, in European barn swallows, *Hirundo rustica* (Møller 2004), warmer spring conditions as a result of climate change have led to an increase in levels of protandry, presumably because they have lessened the survival costs of early arrival and, therefore, allowed sexual selection to promote earlier male arrival. This result, however, has not been repeated in other systems (Rainio et al. 2007). Whether these discrepancies are due to differing magnitudes of between-sex genetic correlations is currently not known.

In addition to the direct influences on t^* and levels of protandry, climate change may have indirect effects through its influence on spatial distributions. Many populations have shifted poleward and/or to higher elevations in response to climate change (Parmesan 2006), and previously isolated populations are now coming into contact as a result. To our knowledge, no assessment has been made of how this may affect mating systems, but conceivably reproductive communication (Ptacek 2000; Slabbekoorn & Smith 2001) and isolation mechanisms (Nei et al. 1983; Palumbi 1994), as well as patterns of hybridization (Harrison 1993) and even speciation (Schluter 2000; Templeton et al. 2001) could all be influenced. We encourage researchers working in these newly established convergence zones to investigate the behavioural mechanisms underlying interpopulation mixing or isolation.

While the number of investigations of the impacts of climate change on mating systems is still limited, the search for general trends needs to begin with standardized methods of quantifying mating systems. The t^*/I_{mates} (as well as m^*) relationships represent a promising avenue. Estimates from long-term individual-based studies, especially, should provide valuable insight into temporal variation.

POLLUTION

Since Carson (1962) set the stage for the modern environmental movement, impacts of pollution on ecosystem health and viability have been a central theme of conservation research. In addition to obvious 'high exposure effects' (e.g. toxicological effects), it is now clear that pollution can affect individuals and populations even with low, sublethal exposure (Lurling & Scheffer 2007; Ward et al. 2008). Indeed, sublethal effects may be more insidious than direct toxicity because, while highly polluted systems tend to be localized, virtually all terrestrial and aquatic ecosystems are contaminated at some level (e.g. Barrie 1967; Landers et al. 1995). Likely effects of sublethal exposure on mating systems fall into two broad categories: (1) physiological/morphological changes to individuals due to endocrine disruption during development (e.g. Colborn et al. 1993; Zala & Penn 2004); and (2) interference with reproductive communication signals (Patricelli & Bickley 2006). These categories are most likely to influence mating systems directly by increasing m^* via an altered sex ratio, or reducing m^* by effectively reducing the receptivity of females to males. However, pollution may also alter t^* by disrupting the time and/or energy budgets of individuals, thus reducing investment in reproduction (e.g. Rabin et al. 2006).

Feminization (i.e. changes in anatomy, physiology and behaviour of individuals and even conversion of developing embryos to female; Bögi et al. 2003; Zala & Penn 2004) via exposure to endocrine disrupting chemicals (EDCs), has been reported in laboratory and field studies for fish (Kime 1998), amphibians (Kloas et al. 1999; Bögi et al. 2003), aquatic reptiles (e.g. Bergeron et al. 1994; Guillette et al. 2000), and semiaquatic and terrestrial birds (Fry & Toone 1981; McCarty & Secord 1999a, b). EDCs can exert a diversity of effects (even including masculinization; Howell et al. 1980) by inhibiting or stimulating endocrine receptors and altering storage, synthesis and/or metabolism of a suite of hormones (Zala & Penn 2004). Consequences at the individual level can include changes to secondary sexual characteristics and reproductive organs, and abnormalities in reproductive behaviour (Guillette et al. 2000; reviewed by Zala & Penn 2004). At the population level, endocrine disruptors could skew operational sex ratios leading to similar population consequences as those following habitat fragmentation (i.e. increasing both m^* and I_{mates}). Alternatively, if frequencies of male traits attractive to females are reduced by EDC pollution, this could cause the opposite effect by effectively reducing m^* .

Changes in secondary sexual characteristics and reproductive behaviour caused by exposure to EDCs may also impair the ability of signallers to communicate their quality to receivers, or alter the preferences of receivers for certain types of signals (Zala & Penn 2004; Lurling & Scheffer 2007). Extremely low-dose exposure (in the parts per billion range) to residues of the pesticide endosulfan disrupts pheromonal signal reception in male red-spotted newts, *Notophthalmus viridescens*, leading to altered mate selection and reduced reproductive success (Park et al. 2001; Park & Propper 2002). Similarly, in mud snails, *Nassa obsoleta*, exposure to organotin compounds can lead to hermaphroditism, but, even in individuals showing no morphological signs of this effect, responses to gender-specific pheromonal signals were reduced (Straw & Rittschof 2004). 4-nonylphenol (4-NP), a common surfactant used during sewage treatment, is toxic at high concentration and can act as an EDC, but only 1 h of exposure at low concentrations caused killifish, *Fundulus diaphanus*, which normally gather in large shoals, to avoid conspecifics (Ward et al. 2008). 4-NP caused no apparent change in the ability of killifish to detect signals in general, but rapidly changed the chemical signature of signallers, making them less attractive and even repulsive to conspecifics (Ward et al. 2008). Active avoidance of conspecifics in a species that tends to aggregate in large groups clearly has the potential to reduce encounter rates, interfere with mate selection and effectively isolate males and females, reducing m^* and I_{mates} .

Visual and acoustic signals can also be disrupted by pollution from urbanization, industry, resource extraction and other human activities. The remarkable diversity of cichlid fish in Lake Victoria, east Africa, for example, declined in the 1980s partly due to interference with visual signals critical for mate choice. Increased turbidity led to reduced coloration of fish, reduced numbers of colour morphs, increased hybridization and, ultimately, reduced species diversity (Seehausen et al. 1997). In undisturbed systems, communication signals tend to be adapted to local environments to avoid masking or interference. Acoustic signallers avoid frequencies that are readily masked by ambient noise (e.g. wind, moving water), or the signals of conspecifics and heterospecifics (Rabin & Greene 2002; Rabin et al. 2003). As in chemically toxic environments, individuals of a wide range of terrestrial and aquatic species may also retreat from historically favourable habitats to avoid anthropogenic noise (e.g. Van Dyke et al. 1986). Noise pollution also has the potential to elevate physiological stress and/or vigilance, which could result in fewer mating attempts and/or altered mating behaviour. Rabin et al. (2006) showed that California ground squirrels, *Otospermophilus beecheyi*, living close to industrial-scale wind turbines showed heightened vigilance and antipredator behaviour relative to controls, both of which could influence the mating system by reducing the time available for mating, effectively reducing t^* and increasing I_{mates} .

A number of species can adjust signals in response to anthropogenic noise. Both great tits, *Parus major*, and song sparrows, *Melospiza melodia*, modify their songs in urban environments to avoid masking by ambient noise (Slabbekoorn & Peet 2003; Wood & Yezerinac 2006). Under these conditions, the most adaptable males may gain greater access to females and, if song flexibility is heritable, this could cause a major change in the genetic make-up of the population. However, if males are flexible and able to produce songs that are readily distinguishable from ambient noise, they may be detected by more females, but if female mate choice is inflexible, these males may be assessed as less attractive, leading to fewer mating opportunities and reduced reproductive rates (Patricelli & Blickley 2006). Again, this would effectively reduce receptivity of females and, therefore, m^* . Males that adjust their songs may also be assessed as less of a threat by other males, leading to more male–male encounters, leaving less time and

energy for mating, effectively reducing t^* , with similar consequences as the indirect effects of disturbance. If altered acoustic signals are strongly favoured by sexual selection, this could lead to reproductive isolation from nearby conspecifics in less noisy rural environments and even speciation if natural selection favours local adaptations to urban versus rural habitats and habitat fragmentation near urban areas reduces gene flow (Patricelli & Blickley 2006; Wood & Yezerinac 2006). To our knowledge, the selective implications of anthropogenic noise pollution have not yet been quantified and many questions exist; for example, whether redundancy in signalling mechanisms and mate selection criteria could allow signallers to shift from one sensory modality to another. Could males increase their reliance on visual displays in the face of acoustic masking, and what are selective implications of these changes for mate choice and fitness (Patricelli & Blickley 2006)?

SELECTIVE HARVESTING

In animal populations, sexual selection often manifests through male–male competition and mate choice by females, thereby resulting in extreme sexual dimorphism (Clutton-Brock 1989). As a consequence of elevated I_{mates} , selection tends to favour adaptations (e.g. large body size, increased size or prominence of weaponry) that allow males to defend sexually receptive females or the resources upon which females rely in female defence mating systems (Quinn & Foote 1994; Pelletier & Festa-Bianchet 2006; Kelly 2008b). Among species that are deemed commercially or recreationally desirable, it is these very traits that are generally targeted for harvesting. Commercial fishing and hunting often remove the largest individuals from the population, a tendency that is reinforced by the minimum size restrictions frequently included in harvesting regulations (Law 2000; Ashley et al. 2003). Recreational hunters and fishers also engage in selective harvesting when they target those individuals with the most extravagant secondary sexual characters. Trophy hunting of various ungulates, including bighorn sheep, *Ovis canadensis*, Dall sheep, *Ovis dalli*, white-tailed deer, *Odocoileus virginianus*, mule deer, *Odocoileus hemionus*, moose, *Alces alces*, and European red deer, *Cervus elaphus*, serves to selectively remove males with the largest horns or antlers (Harris et al. 2002; Coltman et al. 2003; Milner et al. 2007). Moreover, as horn and antler size are often genetically correlated with body size (Coltman et al. 2005), even if trophy hunters do not specifically target the largest-bodied animals, they nevertheless indirectly eliminate them from the population.

One of the assumptions underlying hunting and fishing regulations that favour selective harvesting (Law 2007) is that smaller individuals are younger and therefore possess a greater residual reproductive value (Clutton-Brock 1984), while the largest individuals are the oldest and more likely to be reproductively senescent (sensu Nussey et al. 2006). However, studies of numerous fish populations have shown that harvesting practices that target large body size also tend to remove individuals with high growth rates, as faster-growing fish reach harvestable size earlier in their lives (Swain et al. 2007). Biro & Post (2008) even suggest that fishing directly selects against individuals with fast growth rates, as they tend to be more aggressive and to spend more time feeding than slower-growing conspecifics. Fish that allocate more energy to somatic growth rather than to early reproduction may reach harvestable size before becoming sexually mature, and are therefore less likely to reproduce successfully. Furthermore, fish with fast growth rates and increased size at maturity tend to have higher fecundity, meaning that the individuals with the highest reproductive potential are the most likely to be removed through selective harvesting (Conover & Munch 2002; Willson 2002; Biro & Post 2008).

When selective-harvesting practices are sustained over a significant period of time, they can exert a strong selective pressure and can potentially create a microevolutionary trend running counter to the direction predicted by sexual selection (Hutchings & Rowe 2008). Evidence of such rapid microevolution has been obtained from a population of Atlantic silversides, *Menidia menidia* (Conover & Munch 2002). Harvesting the largest 90% of a population over four generations resulted in the evolution of fish with reduced biomass and growth rate that produced smaller eggs and slower-growing larvae. Likewise, prior to the implementation of the moratorium on the Atlantic cod, *Gadus morhua*, fishery, it was observed that individuals were maturing earlier and at smaller sizes (Barot et al. 2004; Olsen et al. 2004). Harvesting of large pandalid shrimp, *Pandalus borealis*, a sequential hermaphrodite, has produced individuals that change sex earlier and at smaller sizes (Charnov 1981). Rapid phenotypic evolution, typically towards reduced body size and slower growth, has also been documented in Pacific salmon, *Oncorhynchus* spp., halibut, *Hippoglossus hippoglossus*, sole, *Solea solea*, and flatfish (order Pleuronectiformes) (Haug & Tjemsland 1986; Law 2000; Ashley et al. 2003; Walsh et al. 2006). Furthermore, Coltman et al. (2003) noted that the temporal decline in body mass and horn size in harvested bighorn sheep fit with quantitative genetic predictions (using the Breeder's equation; Falconer & Mackay 1996) of microevolutionary change.

The observation that humans can have a demonstrable influence on evolution in animal populations has important implications for conservation and management. Perhaps most importantly, it has been noted that eliminating the harvest of a particular population does not guarantee the reversal of the evolutionary trend towards undesirable trait outcomes, as large-bodied and fast-growing phenotypes may have disappeared from the population (Hutchings & Reynolds 2004; Swain et al. 2007). A classic example is provided by the Atlantic cod, which has failed to rebound despite 15 years of severe restrictions to the fishery (Swain 2011). If much of the genetic variation contributing to large body size or rapid growth has been removed from a given population, the evolutionary return to 'normal' will be impeded (Falconer & Mackay 1996). Undoubtedly, the logic behind selective-harvesting regimes that specify minimum size limitations should be brought into question. In some cases, there is cause for optimism. For example, new regulations favouring the harvest of individuals of intermediate size have already been implemented in both the sturgeon, *Acipenser medirostris*, sport fishery in Washington State and the Maine lobster, *Homarus americanus*, harvest (Law 2007).

The considerable sexual dimorphism and strong sexual selection in mating systems with elevated I_{mates} renders populations showing these forms of mating systems the most vulnerable to selective harvesting. The removal of the most desirable mates from these populations is liable to disrupt patterns of mate choice, intrasexual competition, dominance hierarchies and/or group stability (Rowe & Hutchings 2003; Whitman et al. 2004). In addition, selective harvesting of certain individuals may indirectly create a selective pressure against other members of the population. For example, harvesting of male dungeness crabs, *Metacarcinus magister*, has reduced the number of large males in the population, and since female crabs preferentially choose males larger than themselves, the largest (and presumably most fecund) females are now experiencing difficulty in finding mates (Smith & Jamieson 1991). Ultimately, if those males most capable of defending multiple mates are continuously removed from the population, the stability of defence mating systems and thus the viability of these populations are likely to suffer from continued selective harvesting.

CONCLUSIONS AND FUTURE WORK

The examples above detail four categories of anthropogenic influence on natural animal mating systems, while illustrating the utility of the theoretical and quantitative frameworks of Emlen & Oring (1977), Shuster & Wade (2003) and Wade (1995). We have explicitly placed our review in the context of Emlen & Oring's (1977) ecological classification of mating systems. While this classification system acknowledges the importance of phylogenetic history for mating system variation, it places priority on the contribution of ecological variables. It is the relative contribution of these influences that will, of course, determine the flexibility of mating systems in response to anthropogenic influence. Should phylogenetic inertia be strong, mating systems will be relatively inflexible. However, a number of the above examples show the rapidity with which mating systems can change and, therefore, formulated predictions may serve as useful starting points to test against observed responses.

For simplicity, we have addressed each of the categories of influence in isolation. However, many populations will clearly be exposed to these influences simultaneously. For example, habitat fragmentation that isolates individuals, selective harvesting of dominant males, and impeded reproductive signalling due to pollution could conceivably work in concert to severely disrupt female-defence mating systems. If individuals are then forced to select mates from a smaller pool of candidates, individuals of lower quality, which otherwise would have been excluded, may gain reproductive opportunities. As a result, declines in population viability or undesirable evolutionary consequences are possible (e.g. Coltman et al. 2003). For populations already at risk, these combined impacts (by acting as mechanisms contributing to Allee effects; Allee 1931) could exacerbate the direct effects of, for example, habitat loss and thereby hasten further declines (Rowe & Hutchings 2003). Quantifying the relative contributions of these impacts, while challenging, will thus be of important applied relevance.

As disheartening as they may be, in many cases, human impacts on the environment have created novel research opportunities that can shed light on the proximate mechanisms underlying mating system function. Calls have been made to experimentally manipulate agents of selection in the wild (Wade & Kalisz 1990), but the logistical difficulties of doing so have limited these types of studies. In many cases, anthropogenic influences have created 'natural experiments', and we urge animal behaviour researchers to take advantage of these opportunities. Broad-scale habitat modification has created a complex palette of variation in spatial resource distributions that can be used to explicitly quantify the hypothesized relationships between m^* and mating system variation. Similarly, altered phenologies resulting from climate change may allow for evaluations of how t^* influences mating systems. The feminizing effects of EDCs, and consequent dramatic skews in operational sex ratios, allow for investigations of how sexual selection operates under conditions of extremely variable mate availability. Selective harvesting, for its part, provides opportunities to quantify rates of contemporary evolution in response to readily identified selection pressures. Anthropogenic influences on the natural world are so ubiquitous that the field sites used by animal behaviour researchers are almost inevitably affected. As a consequence, these types of studies are readily feasible and, indeed, potentially unavoidable.

Despite repeated calls for improved connections (e.g. Sutherland 1998; Caro 2007), animal behaviour and conservation biology still remain relatively disengaged. With respect to mating systems, although anthropogenic influences can have important and often predictable effects, they have only recently begun to be

appreciated (Rowe & Hutchings 2003; Eckert et al. 2009). Part of the resistance probably reflects the divergent focus of the two disciplines. Animal behaviour focuses on fitness consequences of individual phenotypic variation, and conservation biology is directed at the preservation of populations. Reproduction, however, is fundamental to both individual fitness and population demography, and we have described a range of ways that an understanding of this commonality (operating through mating system function) can inform applied endeavours and, in turn, how the study of populations affected by human impacts can shed light on mating system function. In our view, the framework outlined above can help to clarify these mechanisms for many species and represents a promising link between conservation and animal behaviour.

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