

Conservation and animal welfare issues arising from forestry practices

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Abstract

Forestry practices may directly kill animals as well as destroy and fragment their habitat. Even without habitat destruction, logging and its associated forest management practices (which include road building, re-forestation, and often increased recreational use) create noise, frighten animals, and may lead to changes in species composition as well as evolutionary responses to the myriad of anthropogenic impacts. Thus, forestry practices may create conservation problems. Forestry practices may also create welfare problems that may act on different temporal and spatial scales than the conservation problems. The individuals affected by forestry may have heightened glucocorticoid levels that may lead to a predictable set of deleterious consequences. Individuals may no longer be able to communicate, or they may no longer be attractive to potential mates. Such welfare problems may generate conservation problems if fitness is reduced. Identifying the set of possible impacts is the first step towards improving welfare and aiding wildlife conservation in managed forests.

Keywords: animal behaviour, animal welfare, conservation, forestry, human impacts, stress

Introduction

Logging, like other human activities, may influence the natural behaviour of forest-dwelling species. These impacts on behaviour may have consequences for individuals, as well as for the populations of affected species; thus, there is likely to be a relationship between welfare and conservation (Bradshaw & Bateson 2000). Impacts on individuals may create welfare issues if pain or suffering increase, or if individual survival decreases in a way that involves physical or emotional injury to the animals (*sensu* Dawkins 1980). The sum total of these welfare issues may create conservation issues if populations decline. Thus, there may be both welfare and conservation impacts from logging and forestry practices, and these impacts may act on different temporal and spatial scales. Although conservation biologists usually focus on broad-scale conservation impacts, the conservation impacts may emerge from the summation of a series of welfare problems acting at the level of individuals. In this somewhat speculative essay, I will define some behavioural and ecological consequences that might follow logging, and then describe some of the forest management practices and point out which practices might create which impacts. My list of potential impacts (and forestry practices) is necessarily incomplete. However, identifying a set of possible impacts is the first step towards improving welfare and aiding wildlife conservation in logged areas.

I acknowledge at the outset that some disturbance is natural in forest ecosystems, and that forest-dwelling species may

have evolved adaptations to disturbance. Moreover, in single-aged, single-species stands of managed forests, some cutting or other forestry practices might mimic natural disturbance and enhance diversity. However, not all forestry and logging is managed or legal.

Logging and other forest management practices (both legal and illegal) modify the environment that animals have presumably evolved in and, thus, could cause rapid evolutionary change. This is because logging is a selective force and evolution may happen on relatively short timescales. Most evolutionary biologists now accept that rapid evolutionary changes can occur (Smith & Bernatchez 2008). In response to changes created by forest management and logging, individuals possessing some traits may prosper while others may fail to thrive. In response to logging, some species will go locally extinct, while others may undergo rapid evolutionary changes in adapting to the human-altered environment.

Potential consequences of anthropogenic disturbance

Mortality

Forest management practices may result in the death of individuals. These deaths may be direct — for instance when an animal is living in a tree that is felled, or hit by a logging truck. They may be indirect — for instance when logging increases fire susceptibility (Holdsworth & Uhl 1997), or forces animals to forage in unsafe areas, or frightens animals and therefore increases glucocorticoid

levels so much that the animals have a suppressed immune system and are thus more susceptible to parasites and pathogens. Many of the behavioural consequences of logging, which are most relevant to the welfare consequences, work indirectly, rather than directly, and ultimately may be responsible for increased suffering and ultimately the death of individuals. Some of these are discussed below.

Habitat destruction

In the short term, at least, logging destroys habitat. This is especially pronounced for species that obligately use forests. For instance, cavity-nesting birds lose breeding locations. Many animals employ a win-stay-lose-shift strategy when selecting breeding sites (Switzer 1993). This means that they will initially return to those sites where they were successful in the past. For these species, animals may return and find no nesting opportunities and then must search for new sites. Since nesting success is often associated with settlement date (ie, first-returning birds may have a selective advantage), birds suddenly forced to find a new place to nest may not fare well that year. In northern boreal forests, birds may have only a single breeding opportunity that must occur over a relatively limited time. Returning and finding no nest sites could be stressful and result in failure to reproduce. And, if trees are cut down during a nesting season, young may perish and parents may be unable to re-nest.

Habitat selection theory tells us that observed patterns of habitat selection are likely to have evolved to maximise individual survival and fecundity (Kotler & Brown 1988; Stamps & Swaisgood 2007). When preferred habitat is destroyed, individuals may be able to move to sub-optimal habitat, but they may be less likely to survive and reproduce. Thus, population fitness may decline as a function of logging-related habitat shifts. A consequence is that the population size may also decline and such declines may decrease the likelihood of population persistence.

Habitat fragmentation

By cutting blocks of trees and creating logging roads, forestry practices may fragment a formerly contiguous habitat. Numerous experimental studies have looked at the viability of animals in newly fragmented habitat (Lawrence & Bierregaard 1997; Debinski & Holt 2000). The effects of fragmentation are not uniform (Debinski & Holt 2000) and may be species-specific, but we generally expect fragmented habitats to contain fewer animal species.

Small fragments may not be able to support a top predator. Sometimes, the presence of a top predator keeps the population of smaller predators from expanding. The loss of the top predator in a fragmented patch leads to the increase in the number of mid-sized predators ('mesopredators'). Since large predators eat large prey and smaller predators eat smaller prey, this 'mesopredator release' can be detrimental to smaller prey. Examples of mesopredator release have been demonstrated in coastal sage patches in southern California, where house cats (*Felis domesticus*) and raccoons (*Procyon lotor*) eat songbirds. In patches with coyotes (*Canis latrans*), there are fewer house cats and

raccoons (because coyotes eat them) and there are more songbirds (Crooks & Soulé 1999). An over-abundance of predators may create welfare problems among prey animals (the sight of a predator can stimulate an endocrinological stress response; Cockrem & Silverin 2002), and have consequences for conservation. Mesopredator release is also implicated in the endangerment and extinction of Australian small mammals (Johnson *et al* 2006). In this case, the crash of dingos (*Canis lupus dingo*) allowed populations of introduced red foxes (*Vulpes vulpes*) and cats to explode. These species efficiently hunted small and mid-sized mammals and therefore triggered their crash. Thus, mesopredator release creates a welfare problem (living around many predators is likely to be stressful) as well as a conservation problem (populations crash).

Road creation

The construction of roads associated with logging can increase mortality of resident mammals, amphibians, reptiles, and birds. Road development and improvement increases the likelihood of vehicular accidents. For instance, in Tasmania, a population of Tasmanian devils (*Sarcophilus harrisii*) almost became extinct after a road was paved (Jones 2000). Vehicle speed increased (because of the road improvement) and drivers were less able to avoid the devils at the higher speeds.

Roads also facilitate the movement of predators, poachers, and competitors. I watched wolves (*Canis lupus*) move along high-elevation logging roads on Vancouver Island. In 1997, when I worked there, these logged areas had some remnant populations of the critically endangered Vancouver Island marmot (*Marmota vancouverensis*) and the wolves preyed on the marmots. It is well known that wolves, and other species, move along roads when it is energetically advantageous to do so, such as when faced with a choice of walking through deep snow.

Roads also facilitate the movement of poachers and the movement of bushmeat (wild game meat) to markets. Anything that makes it easier to move bushmeat to markets increases the trade in bushmeat and thus is responsible for the loss of more wild individuals.

Further, roads fragment the habitat making it harder for some species to move through the landscape and easier for cowbirds (*Molothrus ater*; a brood parasitic species that lays its eggs in other species' nests) to access formerly 'safe' nests (Gates & Evans 1998). Cowbirds typically lay their eggs within several hundred meters of the forest edge (Brittingham & Temple 1983), and the fragmentation created by roads increases the area easily accessible by cowbirds.

There is a growing literature on gap-crossing behaviour. Some species, among them forest specialists, are often reluctant to move across forest gaps (Rail *et al* 1997; Rodriguez *et al* 2001). For some species, gap crossing is more likely when the only alternative is to travel a long distance around a gap (St Claire *et al* 1998; Bakker & Van Vuren 2004). For an individual reluctant to cross a gap, the decision about whether to expose themselves to some predation risk in the open may be stressful. Individuals of

one sex may be more likely than individuals of another to cross gaps (Norris & Stutchbury 2002). Logging, thus, may differentially affect the mobility of individuals and this may lead to population fragmentation and the various deleterious consequences associated with such fragmentation.

A growing number of studies focus on how to make wildlife bridges and tunnels attractive to wildlife (eg McDonald & St Clair 2004). Thus, in the future, there may be remediation that can reduce the negative impacts of both road-building and clear-cutting on some wildlife species.

Increased fear and stress levels

Forestry practices may create fear (Ripple & Beschta 2004; Brown & Kotler 2007) which, in turn, can have profound impacts on behaviour, welfare, and conservation (reviewed in Lima 1998a,b). This fear is based on a prey animal's assessment of the risk of predation. Formally, predation risk is the product of the probability of an attack by a predator multiplied by the consequences of such an attack (eg Ropeik & Gray 2002). Fear viewed this way requires individuals to assess the likelihood of an attack by a potential predator and the consequence (ie, injury or death) of this attack. As fear increases, individuals should attempt to reduce the probability and/or the consequence of an attack. Thus, predation risk, acting through fear, is a potent selective force that may influence morphological adaptations, habitat selection, resource use, and time allocation.

Since virtually all species must simultaneously eat while avoiding being eaten, the risk of starvation has a large impact on prey behaviour: hungry animals take greater risks (Bednekoff 2007; Brown & Kotler 2007). Simultaneously, frightened animals may avoid taking risks. Risk avoidance may include using only 'safe' portions of the habitat. Thus, it is through foraging that the indirect consequences of fear can be identified and understood.

Prey animals should avoid habitats with a greater probability of predation. For example, ungulates living in an area with active logging may forage close to cover to reduce risk. A logical consequence of selective foraging is that the vegetation that they forage on will be more heavily exploited close to cover. In most systems, the population-level consequences of these non-lethal effects are unknown (Lima 1998b).

Forestry practices may elevate glucocorticoid levels in animals. Normally, energy for growth, defence and reproduction are regulated by the hypothalamic-pituitary-adrenal axis (HPA) — a set of linked endocrine glands that work together to modulate energy allocation. When animals are suddenly stressed, energy allocations are temporarily modified to ensure survival. Such 'allostasis' is normal (Goymann & Wingfield 2004). However, chronic stress has a variety of potentially deleterious effects.

Stress may negatively affect the immune system and thus make animals more susceptible to disease (Wingfield & Ramenofsky 1999). Animals must allocate energy to growth, immune defence, as well as to things that ensure their safety. When animals are stressed, they tend to allocate energy to survival and this necessarily means that there will be less energy for growth and immune defence. Thus, chronic stress can lead to immunocompromised animals.

Stress may also be responsible for failure to breed (Wingfield & Sapolsky 2003). Such stress-induced sterility works through both the HPA-axis and the hypothalamic-pituitary-gonadal axis (HPG). Life history theory leads us to expect that reproduction is traded-off against growth and maintenance. Thus, when animals are particularly stressed, they should allocate energy away from reproduction and growth, and mobilise energy to facilitate escape. This reallocation of energy can lead to stress-induced sterility.

In addition to the population-level consequences of stress hormones, these hormones (glucocorticoids) may create anxiety in animals and thus pose an animal welfare concern. We know that glucocorticoids (GCs) create anxiety (feelings of apprehension and fear) because we can modulate glucocorticoid-based responses by injecting humans and animals with GCs, GC agonists, or medications that reduce anxiety in humans (eg Bercovitch *et al* 1995). Moreover, Boinski *et al* (1999) discovered that alarm calls in captive capuchin monkeys (*Cebus apella*) are correlated with the basal corticosteroid levels (which vary among individuals) and thus are a metric by which stress can be quantified; and Blumstein *et al* (2006) discovered that female marmots are more likely to emit alarm calls when they have higher levels of faecal glucocorticoids. Thus, rates of alarm calling could (under similar levels of risk) be used as a non-invasive means of assessing stress in a population.

Individuals that are more likely to call may be exposing themselves to a greater risk of predation if, by calling, they make themselves more detectable to predators. Alarm calls are often easily detectable and may be directed to both predators and prey (Blumstein 2007a); hence, predators may easily locate calling individuals. Thus, increased stress cannot only affect welfare, but it may also affect survival if predators then hunt those animals that are more likely to call.

Increased likelihood of novel and more virulent diseases

Many species have evolved resistance to their parasites and pathogens, and the introduction of new species, with new parasites and pathogens, may have deleterious effects on a local fauna (Altizer *et al* 2001). The increased human movement created by forestry practices may increase the likelihood that resident animals are infected with novel diseases. In addition, logging and logging remediation, such as stream setbacks, may concentrate individuals, thereby increasing contact rates and the potential for disease transmission.

There is a relationship between transmissibility and virulence. Anything that enables a parasite or pathogen to be transmitted more easily can lead to an evolutionary increase in virulence (Ewald 1991). Virulence is defined either as the pathogen's reproductive rate, or the mortality associated with a particular pathogen: by either definition, an individual infected with a virulent pathogen is likely to be worse off than one infected with a less virulent one. If forestry practices increase transmissibility, then they will select for increased virulence. Increased virulence is both a welfare concern and, especially for potentially fatal pathogens, a conservation concern.

Changed mix of personality types

Logging changes selective pressures acting on animals and may change the mix of personality types living in an environment. Non-humans, like humans, behave in consistent ways in different situations — thus they may have personality types (Sih *et al* 2004; Réale *et al* 2007). This intraspecific variation was previously treated as statistical noise, but behavioural ecologists and animal welfare scientists now realise that these personality types may be adaptive and useful for management (Koolhaas *et al* 1999; Smith & Blumstein 2008). For instance, bold individuals may reproduce more rapidly while shy individuals may live longer because they take fewer risks.

The mix of personality types may be important in ensuring population persistence, and habitat or temporal variation may maintain personality-type variation. For instance, in some years, certain personality types may be selectively maintained while, in other years, they may be selected against. Changes in the distribution or abundance of predators, or habitat features, may be important in influencing the mix of phenotypes in a given larger population. Importantly, a mix of phenotypes may ensure population persistence because it provides resilience (Sih *et al* 2004).

Changing the mix of personality types may also have welfare implications. For example, being in a population of hyper-aggressive individuals could expose individuals to high levels of aggression and aggression-related injuries. If fluctuating selection has maintained a mix of personality types, anything that disrupts this could be deleterious for the animals involved because it will select for a certain type of individual, rather than a mix of types.

Interference with communication

Logging creates noise! Trucks, helicopter cranes, and chainsaws all modify the acoustic environment. Modified environments will support different mixes of species. In rainforests, there is often so much background insect noise that it may be too loud to communicate clearly (Mathevon *et al* 2008). Changes in the habitat structure and thermal regime created by logging may influence the distribution and abundance of forest insects (Holloway *et al* 1992; Lawton *et al* 1998; Hill 1999), and thus the background noise through which animals must communicate (Slabbekoorn 2004).

There is abundant evidence that species' acoustic communication systems have evolved to facilitate message transmission through the physical and biological habitat in which they live (Slabbekoorn & Smith 2002; Blumstein & Turner 2005; Brumm & Slabbekoorn 2005). Given that active logging occurs in many locations while birds are defending territories and breeding, the noise created by logging may well interfere with effective communication. And, birds suddenly finding themselves in different thermal environments with different insects may find themselves literally unable to communicate with each other.

Several major reviews have documented the effects of civilian (Bowles 1995) and military noise (Larkin undated)

on animals. Many of these sounds are produced during logging. Ears are remarkably sensitive to slight changes in pressure, and loud noises may damage the hearing abilities of animals (Larkin undated). Noise may be a cause of stress (eg Clough 1982) with consequences discussed above. And, there is literature on using noise to displace animals (eg Murton & Wright 1968) to prevent aircraft impacts or to remove animals from orchards or vineyards. Thus, for a number of reasons, the noise directly created by logging may be harmful to wildlife.

Interference with mate choice

Water quality in logged areas declines and turbidity increases. The modalities and signals fish use to communicate with each other evolved, in part, in response to historical patterns of turbidity (Engström & Candolin 2007). In historically turbid environments, certain species have resorted to electrical communication. However, in historically clear environments, fish rely extensively on visual signals. Work in African lakes has demonstrated that cichlids hybridise in areas with increased run-off (Seehausen *et al* 1997). Experiments have demonstrated that this is because of a failure to discriminate among species in areas with enhanced turbidity.

A recent study (Secondi *et al* 2007) found that turbidity directly affected the size of sexual ornaments. In turbid waters, the size of sexually-selected traits in male newts decreased. This effect might reflect the generally higher habitat quality in clear streams, which would facilitate the elaboration of sexually-selected traits, or it could reflect the different signaling environment where sexually selected morphological traits have no benefit. Additionally, the study was unable to disentangle ontogenetic versus evolutionary factors influencing trait distribution. Regardless, the study showed that turbidity can directly affect the expression of sexually selected traits that have evolved to communicate to females and, thus, turbidity can directly affect evolved mate-choice mechanisms.

Fish visual signals and mating systems have evolved, in part, in response to the natural levels of turbidity that they evolved with. Increased erosion and thus turbidity will inevitably affect the naturally evolved communication and mate-choice systems. The population-level consequences of this can include an increase in hybridisation, and thus a reduction in population fitness, or potentially, a reduced probability of breeding.

Increased human contact

Logging may bring people into contact with formerly remote populations, particularly when forest management facilitates recreation. Much has been written about the impacts of recreation on wildlife (eg Pomerantz *et al* 1988; Knight & Gutzwiller 1995). Effects of increased recreation range from direct effects (eg animals are frightened, hit by cars, hunted) to indirect (eg habitat becomes more or less suitable). The exact nature of recreation will determine the impact. However, the creation of logging roads will inevitably make it easier for people to access formerly remote areas.

Table 1 A summary of the relationship between specific forest practices and possible effects. Each of these possible effects can create both welfare issues (at the individual level) and conservation issues (at the population level).

Possible effects	Clear cutting	Selective harvesting	Stream set-backs	Re-planting	Recreation
Kills individuals	x	x			x
Destroys habitat	x	x			
Fragments habitat	x	x	x		
Creates roads and corridors	x	x	x		
Increases fear and stress	x	x		x	x
Increases the likelihood of new and more virulent diseases	x	x	x		x
Changes the mix of personality types	x	x	x	x	x
Interferes with communication	x	x	x		x
Interferes with mate choice	x	x			
Increases human contact	x	x	x	x	x
Changes thermal regime	x	x			

Altered thermal regime

Some invertebrates, such as butterflies and other insects, are exquisitely adapted to their thermal environment and have specific genes that allow them to live within a circumscribed thermal niche (Gilchrist 2000). Sudden changes in the thermal regime will result in massive mortality. If there is sufficient genetic variation, it may also lead to a rapid evolutionary response in thermal genes.

Streams in formerly forested habitats will also have thermal changes. Warmer water holds less dissolved oxygen and, thus, as the water warms, some fish will no longer be able to live there. Thus, in addition to turbidity, changes in the thermal regime in streams can cause local extinction.

Possible effects from specific forest practices

Table 1 summarises how five forest practices may lead to the effects described above. 'Clear cutting' removes all trees in a certain area and could have all of the deleterious effects. Clear cutting is used in both pristine areas with little prior human contact, as well as managed forests. In pristine areas, individuals with a limited history of exposure to humans may be particularly susceptible to disturbance. Under 'selective harvesting', certain trees are targeted for removal. Although fewer trees are removed, there is still considerable anthropogenic noise and traffic associated with selective logging, and roads are often constructed. Again, in pristine areas, individuals with a limited history of exposure to humans may be particularly susceptible to disturbance. 'Stream setbacks' are areas around streams where primary forest is left so as to reduce erosion. These setbacks are clearly a form of fragmentation, although they also might provide a corridor for movement. Movement corridors increase contact between individuals. 'Re-planting' commonly occurs in sustainable forest management. This

involves people driving or flying into the area where the trees are to be replanted and (often) manually planting trees. Succession itself means that we are creating a dynamic environment in which changing habitats may impact specialists. 'Recreation' is often facilitated in managed forests especially because logging trails allow hikers, mountain bikers, and motor vehicles to use formerly inaccessible areas and cause various types of disturbance to animals.

As the ways that individuals respond to forestry are identified, it should be possible to develop individually based models. Individually based models are simulation models whereby agents (individuals) respond to specific inputs using defined rules. These models rely on a proximate understanding of behaviour and such mechanistic models can be used as tools to facilitate management. For instance, Blumstein *et al* (2005) developed an individually based model to study the consequences of human disturbance on breeding birds. The model simulated birds foraging in a protected area. Paths crossed this area and humans walked down the paths at different rates. Different species responded differently to humans. Using this approach, we could identify the most important factors that influenced fitness-related responses like the quantity of food consumed. A similar individual-based modeling framework could be used to help identify and study the consequences of different forestry actions on both conservation (the population level consequence) and welfare (individual level responses).

Is this all too speculative?

A critical reviewer suggested that this entire paper was speculative and that many of the issues I raise are implausible. Admittedly, some of these possible relationships between forest practices and behaviour have not been directly demonstrated. I view this essay as a forward-

looking preview, rather than a review, that identifies possible behavioural consequences of forestry practices so that testable hypotheses can be developed. Testing these hypotheses will allow us to determine whether indeed the practices have deleterious consequences on individuals and, hence, welfare. It is also essential to realise that not all logging is managed. It is possible that by recognising and studying these issues, proper management of forests may minimise welfare issues associated with logging.

Animal welfare implications and conclusion

Welfare issues arising from forest management may act on various timescales. Anything that stresses an individual could be considered to be a welfare issue, and many of these stressors may be brief and localised. However, longer-term stressors, or factors that increase the exposure of individuals to their predators, as well as any stressor that impacts fitness, necessarily impacts a species' population biology and becomes a conservation issue. Not all welfare issues become conservation issues, but all conservation issues may indicate that there are welfare issues.

Whether any or all of these relationships are issues for a given species is an empirical question. I believe that active adaptive management, whereby properly designed experiments are conducted to measure the effect of a management action, is essential not only to determine whether these factors create welfare and conservation concerns, but also to estimate the relative magnitude of the effects (Blumstein 2007b). Such management requires proper controls, something that might worry those that are trying to maximise welfare in the short run. However, when properly conducted, active adaptive management is a rapid way to quickly identify strategies to maximise animal welfare and minimise pain and suffering. I believe that such experiments may be necessary to develop long-term management plans.

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References

- Altizer S, Foufopoulos J and Gager A** 2001 Diseases and conservation. In: Levin S (ed) *Encyclopedia of Biodiversity, Volume 2* pp 109-126. Academic Press: New York, USA
- Bakker VJ and Van Vuren DH** 2004 Gap-crossing decisions by the red squirrel (*Tamiasciurus hudsonicus*), a forest-dependent small mammal. *Conservation Biology* 18: 689-697
- Bednekoff PA** 2007 Foraging in the face of danger. In: Stevens DW, Brown JS and Ydenberg RC (eds) *Foraging: Behavior and Ecology* pp 305-329. University of Chicago Press: Chicago, USA
- Bercovitch FB, Hauser MD and Jones JH** 1995 The endocrine stress response and alarm vocalizations in rhesus macaques. *Animal Behaviour* 49: 1703-1706
- Blumstein DT** 2007a The evolution of alarm communication in rodents: structure, function, and the puzzle of apparently altruistic calling in rodents. In: Wolff JO and Sherman PW (eds) *Rodent Societies* pp 317-327. University of Chicago Press: Chicago, USA
- Blumstein DT** 2007b Darwinian decision-making: putting the adaptive into adaptive management. *Conservation Biology* 21: 552-553
- Blumstein DT and Turner AC** 2005 Can the acoustic adaptation hypothesis predict the structure of Australian birdsong? *Acta Ethologica* 15: 35-44
- Blumstein DT, Fernández-Juricic E, Zollner PA and Garity SC** 2005 Interspecific variation in avian responses to human disturbance. *Journal of Applied Ecology* 42: 943-953
- Blumstein DT, Patton ML and Saltzman W** 2006 Faecal glucocorticoid metabolites and alarm calling in free-living yellow-bellied marmots. *Biology Letters* 2: 29-32
- Boinski S, Gross TS and Davis JK** 1999 Terrestrial predator alarm vocalizations are a valid monitor of stress in captive brown capuchins (*Cebus apella*). *Zoo Biology* 18: 295-312
- Bowles AE** 1995 Responses of wildlife to noise. In: Knight RL and Gutzwiller KJ (eds) *Wildlife and Recreationists: Coexistence Through Management and Research* pp 109-156. Island Press: Washington, DC, USA
- Bradshaw EL and Bateson P** 2000 Animal welfare and wildlife conservation. In: Gosling LM and Sutherland WJ (eds) *Behaviour and Conservation* pp 330-348. Cambridge University Press: Cambridge, UK
- Brittingham MC and Temple SA** 1983 Have cowbirds caused forest songbirds to decline? *BioScience* 33: 31-35
- Brown JS and Kotler BP** 2007 Foraging and the ecology of fear. In: Stephens DW, Brown JS and Ydenberg RC (eds) *Foraging* pp 397-434. University of Chicago Press: Chicago, USA
- Brumm H and Slabbekoorn H** 2005 Acoustic communication in noise. *Advances in the Study of Behavior* 35: 151-209
- Clough G** 1982 Environmental effects of animals used in biomedical research. *Biology Reviews* 57: 487-523
- Cockrem JF and Silverin B** 2002 Sight of a predator can stimulate a corticosterone response in the great tit (*Parus major*). *General and Comparative Endocrinology* 125: 248-255
- Crooks KR and Soulé ME** 1999 Mesopredator release and avifaunal extinctions in a fragmented system. *Nature* 400: 563-566
- Dawkins MS** 1980 *Animal Suffering: The Science of Animal Welfare*. Chapman and Hall: London, UK
- Debinski DM and Holt RD** 2000 A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14: 342-355
- Engström J and Candolin C** 2007 Human-induced water turbidity alters selection on sexual displays in sticklebacks. *Behavioral Ecology* 18: 393-398
- Ewald PW** 1991 Transmission modes and the evolution of virulence with special reference to cholera, influenza, and AIDS. *Human Nature* 2: 1-30
- Gates JE and Evans DR** 1998 Cowbirds breeding in the central Appalachians: spatial and temporal patterns and habitat selection. *Ecological Applications* 8: 27-40
- Gilchrist GW** 2000 The evolution of thermal sensitivity in changing environments. In: Storey KB and Storey JM (eds) *Cell and Molecular Responses to Stress, Volume 1. Environmental Stressors and Gene Responses* pp 55-70. Elsevier Science: Amsterdam, The Netherlands
- Goymann W and Wingfield JC** 2004 Allostatic load, social status and stress hormones: the costs of social status matter. *Animal Behaviour* 67: 591-602
- Hill JK** 1999 Butterfly spatial distribution and habitat requirements in a tropical forest: impacts of selective logging. *Journal of Applied Ecology* 36: 564-572

- Holdsworth AR and Uhl G** 1997 Fire in Amazonian selectively logged rain forest and the potential for fire reduction. *Ecological Applications* 7: 713-725
- Holloway JD, Kirk-Spriggs AH and Yun Khen C** 1992 The response of some rain forest insect groups to logging and conversion to plantation. *Philosophical Transactions: Biological Sciences* 335: 425-436
- Johnson CN, Issac JL and Fisher DO** 2006 Rarity of a top predator triggers continent-wide collapse of mammal prey: dingoes and marsupials in Australia. *Proceedings of The Royal Society B* 274: 341-346
- Jones ME** 2000 Road upgrade, road mortality and remedial measures: impacts on a population of eastern quolls and Tasmanian devils. *Wildlife Research* 27: 289-296
- Knight RL and Gutzwiller KJ** 1995 *Wildlife and Recreationists: Coexistence Through Management and Research*. Island Press: Washington, DC, USA
- Koolhaas JM, Korte SM, De Boer SF, Van Der Vegt BJ, Van Reenen CG, Hopster H, De Jong IC, Ruis MAW and Blokhuis HJ** 1999 Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience and Biobehavioral Reviews* 23: 925-935
- Kotler BP and Brown JS** 1988 Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19: 281-307
- Larkin RP** undated *Effects of Military Noise on Wildlife: A Literature Review*. USACERL: Champaign, Illinois, USA
- Lawrence WL and Bierregaard RO Jr** 1997 *Tropical Forest Remnants*. University of Chicago Press: Chicago, USA
- Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS and Watt AD** 1998 Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391: 72-76
- Lima SL** 1998a Stress and decision-making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27: 215-290
- Lima SL** 1998b Non-lethal effects in the ecology of predator-prey interactions. *BioScience* 48: 25-34
- Mathevon N, Aubin T, Vielliard J, da Silva M-L, Sebe F and Boscolo D** 2008 Singing in the rain forest: how a tropical bird song transfers information. *PLoS ONE* 3: e1580. doi:10.1371/journal.pone.0001580
- McDonald WR and St Clair CC** 2004 The effects of artificial and natural barriers on the movement of small mammals in Banff National Park, Canada. *Oikos* 105: 397-407
- Murton RK and Wright EN** 1968 *The Problem of Birds as Pests*. Academic Press: London, UK
- Norris DR and Stutchbury BJM** 2002 Sexual differences in gap crossing ability of a forest songbird revealed through radiotracking. *Auk* 119: 528-532
- Pomerantz GA, Decker DJ, Goff GR and Purdy KG** 1988 Assessing impact of recreation on wildlife: a classification scheme. *Wildlife Society Bulletin* 16: 58-62
- Rail J-F, Darveau M, Desrochers A and Huot J** 1997 Territorial responses of boreal forest birds to habitat gaps. *Condor* 99: 976-980
- Réale D, Reader SM, Sol D, McDougall PT and Dingemans NJ** 2007 Integrating animal temperament within ecology and evolution. *Biological Reviews* 82: 1-28
- Ripple WJ and Beschta RL** 2004 Wolves and the ecology of fear: can predation risk structure ecosystems? *BioScience* 54: 755-766
- Rodriguez A, Andren H and Jansson G** 2001 Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos* 95: 383-396
- Ropeik D and Gray G** 2002 *Risk: A Practical Guide for Deciding What's Really Safe and What's Really Dangerous in the World Around You*. Houghton Mifflin: Boston, USA
- Secondi J, Aumjaud A, Pays O, Boyer S, Montembault D and Violleau D** 2007 Water turbidity affects the development of sexual morphology in the palmate newt. *Ethology* 113: 711-720
- Seehausen O, van Alphen JM and Witte F** 1997 Cichlid fish diversity threatened by eutrophication that curbs sexual selection. *Science* 277: 1808-1811
- Sih A, Bell AM, Johnson JC and Ziemba RE** 2004 Behavioral syndromes: an integrative overview. *Quarterly Review of Biology* 79: 241-277
- Slabbekoorn H** 2004 Habitat-dependent ambient noise: consistent spectral profiles in two African forest types. *Journal of the Acoustical Society of America* 116: 3727-3733
- Slabbekoorn H and Smith TB** 2002 Habitat-dependent song divergence in the little greenbul: An analysis of environmental selection pressures on acoustic signals. *Evolution* 56: 1849-1858
- Smith BR and Blumstein DT** 2008 Fitness consequences of personality: a meta-analysis. *Behavioral Ecology* 19: 448-455
- Smith TB and Bernatchez L** 2008 Evolutionary change in human-altered environments. *Molecular Ecology* 17: 1-500
- Stamps JA and Swaisgood RR** 2007 Someplace like home: experience, habitat selection and conservation biology. *Applied Animal Behaviour Science* 102: 392-409
- St Clair CC, Bélisle M, Desrochers A and Hannon S** 1998 Winter responses of forest birds to habitat corridors and gaps. *Conservation Ecology* 2: 13
- Switzer PV** 1993 Site fidelity in predictable and unpredictable habitats. *Evolutionary Ecology* 7: 533-555
- Wingfield JC and Ramenofsky M** 1999 Hormones and the behavioral ecology of stress. In: Balm PHM (ed) *Stress Physiology in Animals* pp 1-51. Sheffield Academic Press: Sheffield, UK
- Wingfield JC and Sapolsky RM** 2003 Reproduction and resistance to stress: when and how. *Journal of Neuroendocrinology* 15: 711-724