

# Sex and sociality in a disconnected world: a review of the impacts of habitat fragmentation on animal social interactions<sup>1</sup>

Sam C. Banks, Maxine P. Piggott, Adam J. Stow, and Andrea C. Taylor

**Abstract:** Despite the extensive literature describing the impacts of habitat fragmentation on the distribution and abundance of species, fragmentation effects on life-history strategies have been relatively understudied. Social interactions are important life-history attributes that have fitness consequences for individuals and have been observed to differ among populations in relation to geographic and demographic variability. Therefore, habitat fragmentation is expected to affect social interactions, and these social impacts or responses may contribute to population viability and broad-scale patterns of distribution and abundance in fragmented landscapes. Here we review the emerging literature on this issue. We focus on the impacts of habitat fragmentation that are expected to, or have been observed to, affect social strategies. These include altered resource distribution (e.g., habitat quality, spatial configuration of patches), interspecific interactions (e.g., predator-prey and host-parasite dynamics, human disturbance), and sex (mate availability and inbreeding risk). The studies we cite identified altered social interactions in response to these influences, including changes to home-range overlap, territoriality, group size, and mating systems. The observed changes to social interactions include passive responses, whereby social interactions are affected by constraints introduced by habitat fragmentation, and adaptive social responses to a modified environment. We suggest that future research could focus on individual fitness benefits and on consequences for population viability of altered social interactions in fragmented environments.

**Résumé :** Malgré l'importante littérature qui décrit les impacts de la fragmentation des habitats sur la répartition et l'abondance des espèces, les effets de la fragmentation sur les stratégies démographiques ont été relativement peu étudiés. Les interactions sociales sont d'importantes caractéristiques démographiques qui ont des conséquences sur la fitness individuelle et on sait qu'elles peuvent varier d'une population à une autre en fonction de la variabilité géographique et démographique. C'est pourquoi, on s'attend à ce que la fragmentation des habitats affecte les interactions sociales et que ces impacts ou réactions sociales puissent contribuer à la variabilité de la population et aux patrons de répartition et d'abondance à grande échelle dans les habitats fragmentés. Nous faisons une revue de la littérature récente sur le sujet. Nous examinons en particulier les impacts de la fragmentation des habitats qui affectent les stratégies sociales ou qui pourraient les affecter. Parmi ceux-ci, notons une répartition modifiée des ressources (par ex., la qualité des habitats, la configuration spatiale des taches), les interactions interspécifiques (par ex., la dynamique des relations prédateurs-proies et hôtes-parasites, les perturbations anthropiques) et la sexualité (la disponibilité des partenaires et le risque de consanguinité). Les travaux que nous citons présentent les interactions sociales qui sont modifiées en réaction à ces influences, en particulier des changements dans le chevauchement des aires vitales, la territorialité, la taille des groupes et les systèmes d'accouplement. Les modifications observées dans les interactions sociales incluent des réactions passives dans lesquelles les interactions sociales sont affectées par des contraintes générées par la fragmentation des habitats, ainsi que par les réactions sociales adaptatives aux modifications du milieu. Nous proposons que la recherche future se concentre sur les bénéfices pour la fitness individuelle et sur les conséquences sur la viabilité de la population des modifications des interactions sociales dans les environnements fragmentés.

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**S.C. Banks<sup>2</sup> and M.P. Piggott.** The Fenner School of Environment and Society, The Australian National University, Canberra, ACT 0200, Australia.

**A.J. Stow.** Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia.

**A.C. Taylor.** Australian Centre for Biodiversity, School of Biological Sciences, Monash University, Clayton, VIC 3800, Australia.

<sup>1</sup>This review is one of a series dealing with some aspects of the impact of habitat fragmentation on animals and plants. This series is one of several virtual symposia focussing on ecological topics that will be published in the Journal from time to time.

<sup>2</sup>Corresponding author (e-mail: [Sam.Banks@anu.edu.au](mailto:Sam.Banks@anu.edu.au)).

## Introduction

Habitat destruction and the subsequent fragmentation of remnant habitat are considered among the greatest contributors to recent and potential future extinctions (Tilman et al. 1995; Henle et al. 2004). The conservation of fragmented ecosystems has been a major focus of biological research in recent decades (Henle et al. 2004). The majority of fragmentation research has focused on patterns of species richness and abundance in fragmented habitat, as well as associations between these patterns and landscape variables (Andren 1994; Dunstan and Fox 1996; Laurance 1997; Lindenmayer et al. 1999; Debinski and Holt 2000; Summerville and Crist 2001; Fahrig 2003). A second major focus of habitat fragmentation research addresses the mechanisms by which fragmentation causes these changes in distribution and abundance, such as edge effects (Fletcher et al. 2007), patch-population connectivity (Stacey and Taper 1992; Stow et al. 2001; Tallmon et al. 2002; Banks et al. 2005*b*), resource availability (Hamback and Englund 2005), and genetic diversity (Frankham et al. 2002). However, we do not really understand the precise individual- and population-level processes that determine a species' persistence or decline in fragmented landscapes. Lindenmayer et al. (2003) suggested that a consistent inability to accurately model and predict fragmented habitat population dynamics was at least partly attributable to the influence of landscape structure on life-history attributes. Life-history differences between populations in fragmented and unfragmented habitats may be an important aspect of a species' response to habitat fragmentation. Social interactions constitute a major aspect of life history with important fitness consequences (Roberts 1996; Brown and Brown 2000), thus intraspecific interactions could be expected to play a role in the viability of patch populations. Yahner and Mahan (1997) first suggested that this might be an important and productive area for future research, and cited five published examples of habitat fragmentation affecting sociality and behaviour. Although the literature on this topic is still not extensive, it has grown considerably in recent years. Here we review the current understanding of the impacts of habitat fragmentation on social interactions, as well as its consequences for individual fitness and population persistence.

Intraspecific variation in social behaviour in response to geographic variation in habitat structure, resource availability, predation risk, and other factors has been demonstrated in numerous species (Foster 1999 and references therein). Such studies have shown that altered social behaviour can be adaptive. Fitness benefits associated with behaviours such as mate choice for inbreeding avoidance (Stow and Sunnucks 2004*b*) or grouping as an antipredator strategy (Magurran et al. 1993) have potential impacts on demography and population persistence. Through effects on demography (e.g., local population size, density, and sex ratio), connectivity, resource availability, and interspecific interactions, habitat fragmentation is likely to change the circumstances and selective forces under which intraspecific social interactions have evolved. The rapid pace of environmental change wrought by anthropogenic activities suggests that sufficient time may not be available for adaptive social interactions to evolve in response to the altered conditions. However, rapid evolution of social strategies has been dem-

onstrated in some species in response to experimental changes in habitat and predation risk (Magurran et al. 1993; Foster 1999). In some cases, species responses to environmental change may be inert, or passive, where social interactions are altered in ways that are most likely maladaptive by constraints introduced by habitat fragmentation. In other cases, we might see social interactions adapt to changes brought about by habitat fragmentation.

The scope of our review is fairly broad, essentially encompassing all social interactions among conspecific individuals. We have attempted to place the observed and expected consequences of fragmentation on social interactions in an evolutionary context. Thus, the structure of our review follows the premise that social interactions evolve primarily in relation to three major influences: resource availability, interspecific interactions (e.g., predator or pathogen avoidance), and sex. We review how habitat fragmentation affects these three factors and the subsequent impacts (expected and observed) on the relevant social interactions. In some cases, effects of fragmentation on demography, connectivity, and resource availability can negatively impact on individual fitness and population viability by restricting fitness-enhancing social strategies or giving rise to maladaptive social interactions, either intra- or interspecifically. In other cases, species have either been able to adapt their social responses to the altered conditions or have a built-in resilience towards particular challenges imposed by habitat fragmentation. We discuss species responses to habitat fragmentation, paying particular attention to any indicative patterns associated with life-history traits or other elements of a species' biology, and highlight areas for future research.

## Resource availability

### How does resource availability influence social behaviour?

The abundance and distribution of resources such as food, nest sites, and refuges influence the behaviour of individuals, including individual space use and cooperation or competition among individuals (Slobodchikoff 1984). For instance, the resource distribution hypothesis predicts that the economics of exploiting resources which are patchily distributed over a spatial or temporal scale enable individuals to share resources over a common area without imposing large costs on each other (Macdonald 1983; Carr and Macdonald 1986; Bacon et al. 1991*a*, 1991*b*). The impacts of resource distribution on individual space use may also impact other aspects of social structure such as mating systems (Clutton-Brock and Harvey 1978; Slobodchikoff 1984; Clutton-Brock 1989). For instance, resource availability may influence the degree of monogamy or polygamy through its effect on population density and home-range overlap, which in turn determine the number of potential mates to which an individual has access (Clutton-Brock and Harvey 1978; Clutton-Brock 1989). There is evidence that many species exhibit flexibility or plasticity in their social behaviour in response to changes in resource availability, whether temporal or spatial (Jarman 1974; Foster 1999; Brashares and Arcese 2002). Below we discuss the effects of habitat fragmentation on resource availability that potentially influence the relevant social adaptations.

### How does habitat fragmentation affect resource availability?

Habitat fragmentation may impact intraspecific interactions via two different mechanisms with inter-related effects: resource distribution and habitat connectivity. Fragmentation alters the spatial distribution and the quality of resources available to individuals. For example, patches may be more productive in terms of leaf protein content, as a result of greater light penetration (Ganzhorn 1995). Alternatively, reduced area and increased spatial dispersion of habitat, vegetation changes, and human disturbance may reduce resource availability within habitat patches and across the landscape in relation to home-range size (Ims et al. 1993). The introduction of a potentially hostile matrix through which individuals may not be able to move is also likely to limit access to resources and (or) change the kin structure of local populations and alter intraspecific interactions (Wolff 1995; Walker 2004). Many species have been shown to display flexible social systems in response to resource distribution (e.g., European wild rabbits, *Oryctolagus cuniculus* (L., 1758), Cowan and Garson 1985; red foxes, *Vulpes vulpes* (L., 1758), Cavallini 1996; European badgers, *Meles meles* (L., 1758), Johnson et al. 2001; red squirrels, *Sciurus vulgaris* L., 1758, Wauters et al. 2005). Therefore, the effects of fragmentation on resource distribution have led to an expectation of altered individual interactions in patch populations (Yahner and Mahan 1997). In the following section, we review studies of social responses to altered resource availability resulting from habitat fragmentation. We have grouped the following sections into studies addressing how fragmentation affects interindividual interactions such as home-range overlap and territoriality, group formation, and social relationships with regard to kinship. Studies that have addressed the relevant social behaviours in relation to habitat fragmentation are summarised in Table 1.

### Space use, home-range overlap, and territoriality

Density increases are a typical result of habitat fragmentation, possibly owing to an initial or persistent “crowding” effect (Debinski and Holt 2000) and (or) increased productivity in patches (Greene et al. 2002; Asbjornsen et al. 2004). High population density has been recorded for many species in remnant habitat; for example, small mammals (Bowers and Matter 1997), primates (e.g., Glessner and Britt 2005), and Cunningham’s skink (*Egernia cunninghami* Gray, 1832) (Stow et al. 2001). Responses to increased density vary among species. European badgers and meadow voles (*Microtus pennsylvanicus* (Ord, 1815)) experience an increased frequency of aggressive encounters (Boonstra and Boag 1992; Macdonald et al. 2004). For many species, home-range size is negatively related to density (Andreassen et al. 1998). This may be due to competition-induced territoriality. For example, the increased density in a remnant population of southern hairy-nosed wombats (*Lasiorninus latifrons* (Owen, 1845)) promoted extreme warren fidelity not seen in lower density populations in continuous habitat, perhaps signalling increased competition for burrows, which is a vital resource with high construction costs (Walker 2004). However, changes in home-range size in relation to patch area and density may also be a strategy to “buffer” populations against altered socio-spatial interactions (Bayne and Hobson 2001;

Koprowski 2005). For instance, a positive relationship between patch size and home-range size was observed for the marsupial greater glider (*Petauroides volans* (Kerr, 1792)) in a cluster of recently formed remnant eucalypt patches within a pine plantation (Pope et al. 2004). However, den sharing and home-range overlap characteristics in these patches were similar to those seen in continuous forest (Lindenmayer et al. 2004; Pope et al. 2004), suggesting recent fragmentation over this small spatial scale has not impacted social organization in this species. The studies cited so far involve species in which home ranges are predominantly restricted to within a single patch. The spatial distribution of habitat patches has also been observed to affect social group size in coyotes (*Canis latrans* Say, 1823), with larger group sizes associated with aggregated resource patches and greater patch area (Atwood 2006), suggesting that increased concentration of resources allows home-range overlap between a greater number of individuals and therefore larger social groups.

The potential behavioural responses to impacts of habitat fragmentation on resource availability have to date not been evaluated in relation to their fitness consequences. Spatio-social organization and individual space use in fragmented populations of root voles (*Microtus oeconomus* (Pallas, 1776)) had no effect on demographic factors such as growth rate, proportion of reproductive adults, or sex ratio at the population level (Ims and Andreassen 1999). However, increased density and home-range overlap may have fitness consequences in terms of access to potential mates. Such questions might be answered by comparisons of social impacts of fragmentation among species and in relation to different landscape structures.

### Group size

Group size is, among other things, a trade-off between the costs of reduced foraging efficiency and the benefits of reduced predation risk (Hamilton 1971). In isolated habitat, groups may be smaller because resource availability may not match the requirements for a large group (Onderdonk and Chapman 2000). Alternatively, predation risk might be lower in patches, reducing the benefits of large group size (see the next section). Group size in response to fragmentation has been most extensively studied in primate species. Groups of red-tail monkeys (*Cercopithecus ascanius schmidtii* (Audebert, 1799)) in forest patches were, on average, less than half the size of those in a large reserve, despite there being a crowding tendency in patches (Baranga 2004). Similarly, black and white colobus monkeys (*Colobus guereza* Rüppell, 1835) have significantly lower group sizes in forest patches than in continuous forest (Onderdonk and Chapman 2000). The home-range areas of *Colobus guereza* were also reported to be an order of magnitude lower in patches, a pattern also reported for other primates (Onderdonk and Chapman 2000). In contrast to *C. a. schmidtii* and *C. guereza*, the group size of ursine colobus (*Colobus vellerosus* Geoffroy, 1834) did not differ between habitat fragments and a large reserve population. However, this was proposed to reflect movements between fragments and the reserve (Wong and Sicotte 2006).

### Altered kin interactions

Where the matrix prevents interpatch movements, all

**Table 1.** Summary of studies describing the effects of habitat fragmentation on social behaviours relevant to resource availability and use.

Species	Habitat specialist or generalist	Original habitat type	Matrix	Effect of fragmentation	Social response	Passive or adaptive social response	References
<b>Home range</b>							
Coyote ( <i>Canis latrans</i> )	Generalist	Forest and grassland	Urbanization and agriculture	Altered temporal and spatial dispersion of critical resources	Home-range overlap is more common when resources clumped	Adaptive	Atwood and Weeks 2003
Root vole ( <i>Microtus oeconomus</i> )	Specialist	Meadow	Experimental (mown area)	Rate of interpatch movement distant-dependent	Home-range overlap decreases with patch size and increasing patch isolation; female space sharing directed towards kin	Adaptive	Andreassen et al. 1998
Southern hairy-nosed wombat ( <i>Lasiorhinus latifrons</i> )	Specialist	Semi-arid grasslands or salt-bush	Agricultural	Patch isolation caused increased population density	Increased warren fidelity	Adaptive	Walker 2004
Eurasian red squirrel ( <i>Sciurus vulgaris</i> )	Specialist	Forest	Forestry	Reduced dispersal; females philopatric in fragments but not in large woodlots	Increased territoriality among females	Adaptive	Wauters et al. 1994
Greater glider ( <i>Petauroides volans</i> )	Specialist	Eucalypt forest	Forestry plantation (exotic pine)	Isolation of patch populations; as patch size increases, density decreases and home-range size increases	No change in degree of den sharing or home-range overlap	Adaptive	Lindenmayer et al. 2004; Pope et al. 2004
<b>Group size</b>							
Coyote ( <i>Canis latrans</i> )	Generalist	Forest and grassland	Urbanization and agriculture	Altered temporal and spatial dispersions of critical resources; resources more clumped in urban areas	Group size increases with aggregation of resource patches and greater patch area	Adaptive	Atwood 2006
Cunningham's skink ( <i>Egernia cunninghami</i> )	Specialist	Rock outcrops	Agriculture	Reduced dispersal among outcrops caused increased within-group relatedness	Group size increases with isolation	Passive	Stow and Sumnucks 2004b
Red-tail monkey ( <i>Cercopithecus ascansius schmidti</i> )	Specialist	Rainforest and woodland	Agriculture	Reduced habitat area and patch isolation causes crowding in patches	Decreased group size	Passive	Baranga 2004
Black and white colobus ( <i>Colobus guereza</i> )	Specialist	Tropical forest	Agriculture	No interpatch movement by groups and patch populations may be remnants	Group size significantly smaller in forest patches than continuous forest, and largely constrained by resources within the patch	Adaptive	Onderdonk and Chapman 2000
<b>Kin interactions</b>							
Gray-tailed vole ( <i>Microtus canicaudus</i> )	Specialist	Alfalfa	Experimental (barren)	Increased local female relatedness	Decreased infanticide	Adaptive	Wolff 1995
Bank vole ( <i>Clethrionomys glareolus</i> (Schreber, 1780))	Specialist	Forest-field mosaic	Experimental (enclosures)	Experimental groups set up with related versus unrelated females, as well as heterogeneous males	Greater home-range overlap between related than unrelated females; increased juvenile survival when neighbouring females are kin	Adaptive	Mappes et al. 1995
Southern hairy-nosed wombat ( <i>Lasiorhinus latifrons</i> )	Specialist	Semi-arid woodland	Agriculture	Patch isolation caused increased population density and increased relatedness among females, the dispersing sex	Increased spatiotemporal association among female relatives	Adaptive	Walker 2004

individuals in small populations will be related to some degree after a small number of generations (Frankham et al. 2002). Elevated relatedness in patch populations suffering reduced dispersal has implications for population demography. For example, fitness-enhancing amicable or kin-based behaviours may be a feature in such patches (Ylonen et al. 1990; Mappes et al. 1995). Increased survival and recruitment of gray-tailed voles (*Microtus canicaudus* Miller, 1897) in patches was thought to be due to decreased infanticide in patches with high relatedness among females (Wolff 1995). Thus, kin tolerance may play a role in causing (via demographic improvements) or facilitating (via kin tolerance) the high population densities often associated with fragmentation (Charnov and Finerty 1980; Lambin 1994; Wolff 1995). Demographic isolation and high population density profoundly altered kin relationships in a remnant population of southern hairy-nosed wombats. In stark contrast to their behaviour in continuous habitat, females chose to cohabit with female relatives (Walker 2004).

## Interspecific interactions

### How do interspecific interactions affect social behaviour?

Interspecific interactions affect many aspects of animal life histories, and social adaptations to these interactions have an important contribution to fitness. Interspecific interactions likely to be affected by habitat fragmentation include predation, parasitism, interspecific competition, and human disturbance. Antipredator behaviour is an important component of the social systems of most species, influencing social group size and cohesiveness (Magurran et al. 1993). The antipredator benefits of grouping include defense (Wilson 1971), improved vigilance and communication (Hirth and McCollough 1977; Kenward 1978), and reduction in individual risk through the dilution and selfish herd effects (Hamilton 1971). The fitness consequences of group living are also influenced by the risk of parasitism and disease, whose transmission is generally facilitated by contact among individuals (Cote and Poulin 1995; Loehle 1995). Other social behaviours with fitness consequences relating to pathogens include social avoidance (Behringer et al. 2006), mate choice, and monogamy (Loehle 1995).

### How does habitat fragmentation affect interspecific interactions?

Habitat fragmentation is likely to influence interspecific interactions through its effects on species richness and community composition (Andren 1994; Didham et al. 1998; Miyashita et al. 1998; Debinski and Holt 2000; Boulinier et al. 2001; Gibbs and Stanton 2001; Fahrig 2003; Watson et al. 2004; Hamer et al. 2006). Fragmentation may reduce or increase species richness (Dunstan and Fox 1996; Miyashita et al. 1998; Debinski and Holt 2000; Summerville and Crist 2001; Fahrig 2003) and alter the abundance and density of particular species within patches and across the landscape (Andren 1994; Virgos 2001; Tischendorf et al. 2005). The impacts of fragmentation on species composition, density, and abundance suggest that species interactions will be affected by habitat fragmentation. Such interactions include predator-prey and host-parasite relationships, as well as interspecific competition owing to changes in the presence and

relative abundance of predators or prey (Kareiva 1987; Suarez et al. 1998; Ewers and Didham 2006; Fletcher et al. 2007). Changes to these interspecific interactions also might be induced by altered habitat structure in fragmented systems through the impacts of edge effects (Ewers and Didham 2005; Fletcher et al. 2007). Rates of pathogen transfection are likely to be influenced by the degree of connectivity of host or pathogen populations in fragmented systems. Disturbance by human activity is likely to be increased in fragmented relative to unfragmented habitat (Kupfer et al. 2006), and may be considered an interspecific interaction within the framework of this review. Below we discuss the social aspects of species' potential and observed responses to the impacts of habitat fragmentation on these interspecific interactions (for summary of relevant studies see Table 2).

### Antipredator behaviour

Habitat fragmentation may affect predator-prey interactions through changes in the presence or relative abundance of predator or prey species. Numerous studies have documented the absence of predator species and reduced predation in fragmented habitat (Miyashita et al. 1998; Chalfoun et al. 2002; Ryall and Fahrig 2006). Conversely, increased predation in fragmented habitat, particularly associated with edge effects and (or) exposure to feral predators, has also been detected (Kareiva 1987; Chalfoun et al. 2002; Ries et al. 2004). The precise impacts of fragmentation on predator-prey relationships are influenced by a variety of factors including habitat requirements of predators and prey and the degree of prey specialization by predators. We do not intend to discuss the large body of theoretical and empirical work on this issue (for a recent review of theory see Ryall and Fahrig 2006), but rather to convey its magnitude. In a meta-analysis, Chalfoun et al. (2002) found that 18 of 66 published studies testing edge effects on predator abundance, activity, or species richness showed a significant increase and 3 showed reduced abundance. Of 23 tests of predator abundance in relation to patch size, 6 showed a significant increase and 4 showed a significant decrease. Eight of 14 tests showed higher predator abundance at the landscape scale.

Fragmentation clearly influences the predation risk to individuals and the risk of local extinction, suggesting that a response to changed predation risk has important fitness consequences. The fitness benefits of adapting to increased predation risk are obvious and adaptive social responses have been documented in numerous species (Magurran et al. 1993). Freshwater minnows (*Phoxinus phoxinus* (L., 1758)) from high-predation habitat were observed to shoal in larger, more stable groups than those from habitat with a lower predation pressure, and group sizes in both populations were observed to increase in response to the experimental addition of predators (Magurran and Pitcher 1987). Furthermore, increased predation pressure was observed to influence the mating tactic of male freshwater guppies (*Poecilia reticulata* Peters, 1859) in favour of more "sneaky mating" strategies and change mate-choice preferences of females toward less brightly coloured males (Endler 1995; Houde 1997). The benefits of an adaptive response to relaxed predation pressure are less immediately apparent. However,

**Table 2.** Summary of studies investigating the effects of habitat fragmentation on social behaviours relevant to interspecific interactions.

Species	Habitat specialist or generalist	Original habitat type	Matrix	Effect of fragmentation	Social response	Passive or adaptive social response	Reference
Caribou ( <i>Rangifer tarandus caribou</i> )	Specialist	Woodland	Timber harvesting	Reduced home-range size	Affects "spacing out" antipredator strategy	Passive	Smith et al. 2000
Ten forest passerines ( <i>Parus</i> L., 1758, <i>Aegithalos</i> Hermann, 1804, <i>Certhia</i> L., 1758, <i>Regulus</i> Cuvier, 1809)	Specialists and generalists	Forest	Agricultural	Mixed-species flock sizes reduced in small fragments; increased predation risk	Individual antipredator behaviour of blue tits ( <i>Parus caeruleus</i> ), but no group-level response	Adaptive (individual-level only)	Tellería et al. 2001
American redstarts ( <i>Setophaga ruticilla</i> )	Specialist	Boreal forest	Agricultural	Increase of parasitic birds such as brown-headed cowbird ( <i>Molothrus ater</i> ), which can reduce reproductive output (experimental)	Increased aggression towards models of cowbirds, particularly from females	Adaptive	Hobson and Villard 1998
Mountain gazelle ( <i>Gazella gazella</i> )	Generalist	Coastal plain	Mixed: urban, agricultural, industrial, military	Increased human disturbance and feral animals	Smaller groups and increased individual vigilance	Adaptive	Manor and Saltz 2003
Western roe deer ( <i>Capreolus capreolus</i> )	Generalist	Woodland	Agricultural	Altered habitat structure, increased human disturbance	Group size related to habitat type, but smaller with increasing human disturbance	Adaptive	Hewison et al. 2001

there are trade-offs associated with antipredator strategies, and reduced predation risk might allow for improved fitness through allocation of time to other activities such as foraging or mating and necessitate smaller social groups (Lima and Dill 1990). Freshwater guppies translocated from a high-predation environment to a previously unoccupied low-predation environment were observed to develop shoaling and predator-inspection behaviours similar to those of other low-predation populations (Magurran et al. 1992).

The few published studies on the effects of habitat fragmentation on predator-prey relationships suggest that fragmentation constrains social components of antipredator strategies. In contrast to the adaptive social response described above to increased predation risk, Tellería et al. (2001) found that flock structure of wintering insectivorous forest passerines in fragmented habitat contained fewer individuals and fewer species compared with unfragmented forests. The authors suggested that flock size and composition were affected by ecological restrictions imposed by the small size of fragments, and that an increase in predation risk triggered changes to individual behaviour rather than to the flock. In a study of the response of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) to habitat fragmentation resulting from timber harvesting, Smith et al. (2000) suggested that "spacing out" antipredator behaviour of caribou could be compromised by reduced home-range size in increasingly fragmented habitat. The social components of antipredator strategies may be compromised in fragmented landscapes because of reduced resources such as food and space. In such cases, individual responses to predator risk may become more important. For example, individual blue tits (*Parus caeruleus* L., 1758 = *Cyanistes caeruleus* (L., 1758)) foraged deeper in the canopy and increased scanning and hopping rates in fragmented habitat with an increase in abundance of raptors (Tellería et al. 2001). Hobson and Villard (1998) also observed changes in individual antipredator behaviour in fragmented habitat, where models of the brood parasitic brown-headed cowbirds (*Molothrus ater* (Boddaert, 1783)) resulted in increased aggression in female American redstarts (*Setophaga ruticilla* (L., 1758)).

### Avoidance of parasitism

Habitat fragmentation has been shown to alter host-parasite dynamics in a range of taxa. Taylor and Merriam (1996) detected lower rates of midgut parasite infection of damselflies (*Calopteryx maculata* (Beauvois, 1805)) in fragmented compared with unfragmented habitat. Lower prevalence of ticks (*Ixodes scapularis* Say, 1821) was detected in white-footed mice (*Peromyscus leucopus* (Rafinesque, 1818)) in smaller than in larger habitat fragments in an agricultural landscape (Wilder and Meikle 2004). Conversely, edge effects increased bot fly (*Cuterebra fontinella* Clark, 1827) parasitism of white-footed mice (Wolf and Batzli 2001). As with the impacts of fragmentation on predator-prey interactions, the degree of habitat and host specialization of parasites is likely to be an important factor influencing host-parasite relationships in fragmented systems (Roth et al. 2006). For instance, of three parasitoid wasp species studied, Roth et al. (2006) only found in-

creased parasitism rates in fragmented habitat by *Lespesia frenchii* (Williston, 1889), the broadest generalist with respect to host choice.

Compared with the social aspects of antipredator responses, relatively little work has been done on the role of pathogen avoidance in the evolution of social systems. However, in many cases parasitism may have a larger influence on individual fitness (Loehle 1995; May 1988). Increased risk of pathogen transmission in fragmented habitats may affect mating systems in the form of reduced polygamy or stronger preference for unparasitised mates (often those with brighter colours or more ornamental displays) (Loehle 1995). Increased pathogen risk should also select for contact with fewer individuals and reduced sociality (Cote and Poulin 1995; Loehle 1995). Testing hypotheses about adaptive social responses to changed host–parasite dynamics in fragmented habitat may prove particularly informative, particularly with respect to altered population size, density, and connectivity in fragmented landscapes.

### Response to human disturbance

Human-caused disturbance in fragmented landscape may occur via extractive activities such as forestry or agricultural activities or simply via increased human use of fragmented and settled landscapes (Kupfer et al. 2006). However, even with increasing human disturbance, studies on the impact of human disturbance on biological processes in fragmented landscapes are rare. Several studies have documented impacts on social behaviour in ungulates (Hewison et al. 2001; Manor and Saltz 2003). Manor and Saltz (2003) found a negative relationship between group size and human disturbance in *Gazella gazella* (Pallas, 1766). In open areas with low-disturbance levels, gazelles occurred in bigger groups than in open areas with high-disturbance levels. Furthermore, in heavily disturbed areas, there was evidence of increased individual-vigilance levels in the bigger groups (Manor and Saltz 2003). Behavioural plasticity was also observed in western roe deer (*Capreolus capreolus* (L., 1758)) across an agricultural landscape of differing structure (Hewison et al. 2001). Roe deer avoided areas associated with human activity; average group size was lower in those areas where human disturbance was high. Whether the impact of human disturbance in fragmented landscapes has any fitness consequences requires investigation. However, negative fitness impacts were demonstrated in bottlenose dolphins (*Tursiops truncatus* (Montagu, 1821)), where prolonged human disturbance was associated with individual behavioural changes and population decline (Constantine et al. 2004; Bejder et al. 2006).

## Sex

### How does sex influence social behaviour?

Social adaptations relating to mating systems and sex probably contribute to individual fitness more than any other social behaviour. Access to mates influences behaviours such as territoriality (Tobias and Seddon 2000; Lacey and Wiczorek 2001; Morley and Balshine 2002; Eason and Hannon 2003; Wronski and Plath 2006) and competition among individuals (Hutchings et al. 1999; Eberle and Kappeler 2002; Vasey 2004). Avoidance of inbreeding influen-

ces dispersal strategies (Greenwood 1980), mate choice (Tregenza and Wedell 2000), multiple mating, and polygamy (Johnsen et al. 2000; Tregenza and Wedell 2002). Habitat fragmentation has the potential to affect many of these behaviours. Below we describe documented effects of habitat fragmentation and how these are expected, or have been observed, to affect mating systems of animals (for summary of relevant studies see Table 3).

### How does habitat fragmentation affect mating systems?

First, fragmentation can reduce population size or density at the local (patch) and landscape levels (Debinski and Holt 2000). The small size of local populations and increased dispersion of individuals across the landscape may reduce the number of potential mates available to individuals in fragmented landscapes, and therefore, the number of alternative mate choice options. Through its effects on local population or “neighbourhood” size, habitat fragmentation therefore may affect the success of pair formations (Dale 2001), the rate of extra-pair copulations (Norris and Stutchbury 2001), polygamy, and multiple mating (Banks et al. 2005c; Martin and Martin 2007; Martin et al. 2007).

Second, habitat fragmentation has been documented to alter population sex ratios, either simply through demographic stochasticity in small populations or through increased mortality associated with dispersing across unsuitable habitat by species with sex-biased dispersal (Raska-Jurgiel 1992; Beshkarev et al. 1995; Dale 2001; Banks et al. 2005a; Matter 2006). Biased sex ratios change relative levels of mate availability for the two sexes and may reduce rates of pair formation and reproductive output (Dale 2001). Furthermore, reduced levels of multiple paternity have been detected when populations of the carnivorous marsupial *Antechinus agilis* Dickman, Parnaby, Crowther and King 1998 have female-biased sex ratios (Kraaijeveld-Smit et al. 2002), which has been identified as a consequence of habitat fragmentation (Banks et al. 2005c). Simulations of extinction probabilities demonstrated that polygamy and monogamy confer different risks of extinction in relation to demographic stochasticity and altered sex ratio, with monogamy resulting in a higher extinction risk than a polygynous mating system (Legendre et al. 1999).

Third, habitat fragmentation can reduce dispersal rates between populations by the increased distance required to travel between populations and the degree to which the intervening matrix acts as a dispersal barrier (Doak et al. 1992; Ricketts 2001). The impacts of fragmentation on dispersal have been observed to differ between the sexes, thereby altering the degree of sex bias in dispersal (Stow et al. 2001; Tallmon et al. 2002; Johnson et al. 2003; Banks et al. 2005b). Reduced dispersal and increased isolation of small patch populations can reduce the local “social neighbourhood size” and reduce the number of potential mates available to individuals in fragmented landscapes (Diaz et al. 2006). Aside from the immediate demographic consequences (Stacey and Taper 1992), reduced immigration results in elevated genetic relatedness among individuals in patch populations, increasing the risk of inbreeding (Mills and Smouse 1994; Stow et al. 2001; Banks et al. 2005b).

Fourth, habitat fragmentation can lead to the loss of genetic diversity as a result of genetic drift in small and isolated

**Table 3.** Summary of studies investigating the effects of habitat fragmentation on mating systems.

Species	Habitat specialist or generalist	Original habitat type	Matrix	Effect of fragmentation	Social response	Passive or adaptive social response	References
<b>Mate location and pair formation</b>							
Speckled wood butterfly ( <i>Pararge aegeria</i> )	Generalist	Woodland	Agricultural	Altered habitat structure and population density	Altered mate location behaviour	Adaptive	Mercx and Van Dyck 2005
Ovenbird ( <i>Seiurus aurocapillus</i> (L., 1766))	Specialist	Forest	Agricultural	Fewer potential mates in fragmented habitat	Reduced pair formation	Passive	Gibbs and Faaborg 1990
Kentucky Warbler ( <i>Oporornis formosus</i> (Wilson, 1811))	Specialist	Forest	Agricultural	Fewer potential mates in fragmented habitat (but less sensitive to fragmentation than <i>S. aurocapillus</i> above)	No reduction in pair formation	Passive	Gibbs and Faaborg 1990
Hooded warblers ( <i>Wilsonia citrina</i> )	Specialist	Forest	Agricultural	Reduced opportunity for extra-pair copulation	Males spend increased time out of territories and travel farther; females reduce extra-pair forays	Adaptive (males)	Norris and Stutchbury 2001, 2002
Des Murs' wren-tail ( <i>Sylvioorthorhynchus desmursii</i> )	Specialist	Rainforest	Agricultural	Population connectivity limits access to mates	Reduced pair formation in small isolated patches	Passive	Diaz et al. 2006
Several bird species (meta-analysis)	Various	Various	Various (natural or human-caused population isolation)	Reduced female availability with increasing population isolation	More unpaired males	Passive	Dale 2001
<b>Polygamy and inbreeding avoidance</b>							
Mountain brushtail possums ( <i>Trichosurus cunninghamii</i> )	Specialist	Forest	Agricultural	Increased overlapping of male and female home ranges with population density and patch shape	Change from monogamy to polygyny	Adaptive	Martin and Martin 2007; Martin et al. 2007
Cunningham's skink ( <i>Egernia cunninghamii</i> )	Specialist	Forest	Agricultural or deforestation	Increased relatedness of potential mates	Inbreeding avoidance by mate choice	Adaptive	Stow and Sunnucks 2004b
Agile antechinus ( <i>Antechinus agilis</i> )	Specialist	Forest	Exotic forestry plantation	(i) Increased relatedness of potential mates; (ii) fewer male partners available to females	(i) Behavioural avoidance of opposite-sex relatives; (ii) reduced levels of multiple paternity	(i) Adaptive; (ii) passive	Banks et al. 2005c
<b>Reproductive synchrony</b>							
Root vole ( <i>Microtus oeconomus</i> )	Specialist	Meadow?	Experimental (mown area)	Isolation of patch populations	Reproductive synchrony developed in isolation	Adaptive	Johannesen et al. 2000
Agile antechinus ( <i>Antechinus agilis</i> )	Specialist	Forest	Agriculture	Isolation of patch populations	Reduced reproductive synchrony between patches	Passive	Wallis 2006



patch populations (Hitchings and Beebee 1998; Vucetich et al. 2001). Although effective population size and the rate of genetic drift are influenced by mating systems (Frankham et al. 2002), an adaptive behavioural response to reduced genetic diversity may seem unlikely. However, reduced genetic diversity at the population level increases genetic similarity among potential mates, therefore promoting the benefits of inbreeding avoidance strategies such as mate choice or polyandry as mechanisms of ensuring offspring genetic diversity (Olsson and Madsen 2001).

Fifth, the size and connectivity of patch populations have been implicated in reduced reproductive synchrony within and between populations. In a study of the semelparous marsupial carnivore *A. agilis* in a patch network in agricultural land, Wallis (2006) detected significant differences in birth dates between patches and an association between male population size and reproductive synchrony within patches. In contrast, Johannesen et al. (2000) found that reproductive synchrony only developed within isolated patch populations of root voles, as migrant exchange in spatially proximal patches disrupted female social groups.

Through the above five processes and others, fragmentation has been observed to reduce reproductive output in diverse taxa (Fort and Otter 2004; Diaz et al. 2005; Beck and Heinsohn 2006). These negative consequences of habitat fragmentation for reproductive success imply that the fitness benefits of an adaptive response to fragmentation impact on mating systems. Below we discuss the expected and observed adaptive behavioural responses to the impacts of habitat fragmentation on two major aspects of mating systems: mate availability and inbreeding avoidance.

### Habitat fragmentation impacts on mate availability

Fragmentation has been observed to reduce rates of pair formation in birds through reduced local population size and male-biased sex ratios associated with female migration (Gibbs and Faaborg 1990; Dale 2001). Furthermore, reduction in population connectivity was demonstrated to reduce pair formation in a Chilean forest bird (Diaz et al. 2006). The success rate of finding mates by the Des Murs' wiretail (*Sylviorthorhynchus desmursii* Des Murs, 1847) was dependent on the presence of corridors linking patch populations: only 20% of territories in isolated forest fragments surrounded by pasture were occupied by mated pairs compared with 72% of fragments connected by corridors. In contrast to the results of these studies, increased population densities in fragmented habitat may increase encounters with potential mates. Population density and patch shape may affect home-range overlap among individuals in fragmented systems. In response to increased resource availability and a higher population density in roadside remnant habitat compared with forest habitat, home ranges of female mountain brushtail possums (*Trichosurus cunninghami* Lindenmayer, Dubach and Viggers 2002) overlapped with those of a greater number of males than in the forested habitat (Martin and Martin 2007; Martin et al. 2007). The mating system of the roadside population was polygyny, as opposed to social monogamy in the forest population. These examples demonstrate the potential fitness consequences of the impacts of habitat fragmentation on mate availability. A similar conclusion was drawn by Wells et al. (1998), who used a simulation approach

to demonstrate that mate-location success is based on the Allee effect, in that poorer success rates occurred in smaller populations. This highlights the selective benefits of strategies that increase mating-season population densities or mate-location ability. Models of dispersal and settlement decision-making strategies evaluated by Fletcher (2006) further support this conclusion in demonstrating that conspecific attraction increases fecundity. An adaptive behavioural response to the challenges associated with mate location was detected in the speckled wood butterfly (*Pararge aegeria* (L., 1758)), in which males altered rates of perching and patrolling to increase mate-location efficiency in fragmented habitat (Merckx and Van Dyck 2005). Male hooded warblers (*Wilsonia citrina* (Boddaert, 1783)) were able to maintain access to potential mates for extra-pair copulations by travelling between nearby habitat patches, in contrast to females who reduced their extra-pair forays (Norris and Stutchbury 2001, 2002). These studies highlight behaviours that may assist in maintaining mating opportunities and fitness in fragmented habitat. However, such behavioural responses may be constrained by habitat fragmentation in other circumstances. Norris and Stutchbury (2001) suggested that increased spatial dispersion of habitat patches would decrease the availability of extra-pair partners, a hypothesis supported by rates of multiple paternity in the marsupial carnivore *A. agilis*, which were lower in more geographically isolated patches (Banks et al. 2005c).

### Habitat fragmentation impacts on inbreeding avoidance

Fragmentation may increase inbreeding risk through reduced local-population sizes and restricted dispersal, resulting in elevated genetic similarity among potential mates (Stow et al. 2001; Banks et al. 2005c). Other than dispersal, behavioural strategies to minimise the risk of inbreeding include the recognition and behavioural avoidance of kin, either if familiarity correlates well with kinship or more directly by genetic comparison of self and potential partners (Blouin and Blouin 1988; Bull and Cooper 1999; Shellman-Reeve 2001; Stow and Sunnucks 2004b). Postcopulatory physiological mechanisms for inbreeding avoidance include sperm selection, for example, on the basis of genetic compatibility and (or) heterozygote advantages (Pusey and Wolf 1996; Tregenza and Wedell 2000). This form of cryptic female choice may in fact promote polyandry to increase the probability of a suitable sire(s). Indeed, polyandry has been demonstrated to enhance offspring viability (Tregenza and Wedell 2002).

In organisms that detect and avoid inbreeding, habitat fragmentation has therefore the potential to impact on their mating behaviours. Where genetic relatedness among potential mates is elevated in fragmented habitat, it might be expected that individuals would be buffered against increased inbreeding risk by selecting less-related mates as sires. Indeed, this was observed by Stow and Sunnucks (2004b) in the lizard *E. cunninghami*. Here, *E. cunninghami* was used to investigate inbreeding when habitat fragmentation leads to increased local relatedness. A typical social group of *E. cunninghami* comprises a single, long-term, monogamous pair sharing space with multiple generations of close kin. This social system was little altered by deforestation in

**Table 4.** Summary of studies testing for inbreeding avoidance by mate choice (mates less genetically related than random) in fragmented habitat.

Species	Monogamy or polygamy	Multiple paternity within litter	Inbreeding avoidance response	Reference
Pika ( <i>Ochotona princeps</i> (Richardson, 1828))	Sequential monogamy*	No	No	Peacock and Smith 1997b
Cunningham's skink ( <i>Egernia cunninghami</i> )	Monogamy	No	Yes	Stow and Sunnucks 2004b
Agile antechinus ( <i>Antechinus agilis</i> )	Polygamy	Yes	No	Banks et al. 2005c
Grand skink ( <i>Oligosoma grande</i> Gray, 1845)	Polygamy	Yes	No	Berry 2006

**Note:** Findings are presented in relation to the mating system for the species.

\*No evidence of multiple paternity within a litter, but females have two litters per year and may change partners for the second litter of the season (Peacock and Smith 1997a).

ways that might compensate for the increased potential to inbreed (Stow and Sunnucks 2004a). Even though male-bias in dispersal was stronger in fragmented areas, this did not necessarily support inbreeding avoidance because dispersal was reduced in both sexes (Stow et al. 2001). Nevertheless, no additional inbreeding was observed in deforested habitats. Habitat differences for the level of inbreeding were not evident from either distributions of individual multilocus heterozygosity or the degree of relatedness between identified breeding pairs (Stow and Sunnucks 2004b). Inbreeding avoidance in *E. cunninghami* has therefore been sufficiently strong to withstand the increases in local relatedness brought about by habitat fragmentation. Perhaps some resilience towards increased pressure to inbreed is not unexpected in *E. cunninghami* given an acute ability to detect close kin, most likely owing to its natural structuring into kin-groups and long-term investment in one breeding partner.

However, inbreeding avoidance by mate choice can compromise fitness, by default, because it involves the reduction in the number of potential mating partners (Keller and Arcece 1998). In extreme circumstances, this may lead to a reduced reproductive output in small populations through the "glass effect", whereby individuals refuse to mate with genetically similar individuals (Tainaka and Itoh 1996). Such rigid inbreeding avoidance would be seemingly most likely in species that have evolved in environments with a high risk and cost of inbreeding, such as with the *E. cunninghami* example given above. Indeed, there is some evidence that a glass effect of sorts is beginning in *E. cunninghami*, as greater proportion of nonbreeding male lizards in deforested habitats is most likely a result of mate constraint imposed by elevated relatedness. Inbreeding avoidance, coupled with increased local relatedness, also most likely explains the association of deforestation with male-biased dispersal as a form of "frustrated" dispersal (Stow and Sunnucks 2004b). This is an interesting result in relation to population persistence, as Johnson and Gaines (1987) found that preventing dispersal of prairie voles (*Microtus ochrogaster* (Wagner, 1842)) can modify survival rates, with frustrated dispersers having a lower survival rate than philopatric individuals or individuals allowed to disperse.

If mating opportunities are limited, monogamous species may be more susceptible to lower recruitment than polygamous ones, where mate choice is relatively less important as an inbreeding avoidance strategy (Bessa-Gomes et al. 2003). Indeed, as shown in Table 4, the inbreeding avoidance response of *E. cunninghami* was not detected in fragmented habitat in other studies of polygamous reptiles (Berry 2006) and mammals, even when relatedness among

potential mates was increased (Banks et al. 2005c). Where postcopulatory sperm selection mechanisms exist, reduction of mating opportunities by the avoidance of genetically similar individuals is likely to be less beneficial in terms of inbreeding avoidance than polyandry (Tregenza and Wedell 2002). Future studies of the response to inbreeding of other taxa in fragmented habitat will help elucidate the fitness benefits of different adaptive responses in relation to the various mating systems, and whether fragmentation places any restrictions on inbreeding avoidance behaviours. Banks et al. (2005c) demonstrated that a social response to elevated inbreeding risk (male–female relatedness) by the agile antechinus in fragmented habitat was constrained by population size and nest availability. In large patches, there was behavioural avoidance of opposite-sex relatives in communal nests, a pattern not observed in unfragmented habitat where relatedness among potential nest sharers was lower. However, this behaviour was not detected in small patch populations, despite an even greater average relatedness among opposite-sex pairs, presumably because of the limitations of nest availability and the number of potential nest mates. Furthermore, polyandry as an inbreeding avoidance mechanism was constrained by patch-population size and isolation, as multiple paternity was reduced as a consequence of low male population sizes and patch isolation.

## Conclusions

Studies of social impacts of fragmentation have composed only a minor proportion of fragmentation research to date. Processes are more difficult to study than patterns, and in comparison with information on species occurrence or abundance, the research effort required to collect quality data on social interactions is far greater, which may explain the relative paucity of robust comparisons across habitat contexts. Furthermore, methods that enable the study of some aspects of social systems, such as highly variable genetic markers for the study of mating systems (Hughes 1998), have become available only relatively recently. Nevertheless, this review shows that researchers are beginning to build a picture of the mechanisms by which fragmentation impacts social interactions, including passive responses, whereby social interactions are affected by constraints introduced by fragmentation, and adaptive responses that may increase individual fitness and population viability in response to fragmentation. We now know that many aspects of the impacts of fragmentation, such as those relating to resource quality and distribution, interspecific interactions, patch-population demography, and connectivity, can influence a

variety of social interactions including territoriality, social group size, kin interactions, and mating systems. However, although the number of studies addressing these issues is growing, the published literature is far from adequate to use across-species patterns to draw general conclusions about the social impacts of fragmentation in relation to variation in life-history strategies and landscape contexts. The research on fragmentation impacts on inbreeding avoidance is suggestive of some degree of predictability of mating-system responses in relation to variation in mating strategies. However, studies on a wider range of taxa with a diversity of mating systems are required to make robust generalizations. Furthermore, taxonomic representation among the studies that have been published is strongly biased. Mammal studies comprised 67% of the published papers on social impacts of fragmentation cited in this review. The remainder was dominated by avian studies (21%), followed by reptile and invertebrate papers, comprising 9% and 3%, respectively.

We hope that the observed and predicted interactions between habitat fragmentation, life-history strategies, pre-existing social behaviour, and adaptive social responses that we have described might help researchers to formulate testable hypotheses about the social impacts of habitat fragmentation. A consideration for future research on this issue is the distinction and interaction between passive changes to social interactions induced by constraints associated with habitat fragmentation and adaptive social responses to maximise fitness in response to altered circumstances, such as resource or mate availability, interspecific interactions, or inbreeding risk. From a conservation perspective, the next step after understanding the social impacts of fragmentation relates to the individual fitness costs or benefits of altered social interactions and whether these have any short-term or long-term consequences for population viability in fragmented ecosystems.

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