REVIEW

Population density and the evolution of male aggression

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Abstract

In some cases male animals engage in aggressive contests for access to females, in others they adopt more passive strategies and invest in traits that assist them in detecting females or in competing with rivals in other ways, such as sperm competition. One possible factor determining the fitness of these different strategies is population density. Theoretically, aggressive tactics should be found at intermediate population densities. At low densities males that invest in traits related to searching for mates could be favoured, whereas at the highest densities males that fight over females might pay excessive costs for this behaviour because of the number of rival males that they will encounter. Current empirical evidence is mostly consistent with this scheme: in some cases it seems that traits that are associated with locating mates are favoured at low densities, with aggression related traits favoured at higher densities, and in other cases aggression is selected but as density increases less aggressive strategies become more common. There remain substantial differences between species, however, and I discuss how variation in mating system, in the costs of aggression and in the nature of sperm competition, plus ecological differences between species, can change the relationship between population density and the fitness consequences of aggressive and passive behavioural strategies.

Introduction

Behaviour and ecology are in many ways two sides of the same coin: behaviour determines the nature and rate of almost all of the processes that are studied by ecologists, such as food consumption, aggregation and disease transmission, and ecology feeds back into behaviour in a similar way, meaning that despite the wishes of some researchers it is not advisable to study behaviour without taking ecology into account. Given this very close linkage between behaviour and ecology, it is perhaps surprising that many aspects of this relationship remain poorly studied. Take, for example, those behaviours associated with mating and sexual selection. It has been recognized for some time (Emlen & Oring, 1977) that ecological factors are important in determining the strength of sexual selection within a species, but of these factors only the operational sex ratio (OSR) has been the subject of a focussed (and successful) research programme (Kvarnemo & Ahnesjö, 1996, 2002; Reynolds, 1996). The role of other potentially important aspects of a species' ecology on sexual selection and mating behaviour are less well studied.

The subject of this review is the effect of one of these ecological factors, population density, on a specific aspect of sexually selected behaviour, namely aggressive behaviour between animals competing for mates. Understanding the

relationship between population density and aggression is important not only for our understanding of the evolution of the diversity of life, but also because it may have important conservation or pest control implications. One of the most common effects that humans have on animals is to change their abundance: human activity invariably leads to many species experiencing either much higher or much lower population densities than they would in an undisturbed habitat. If we are concerned about preserving species that have had their abundance reduced, or if we wish to control those species that have increased in numbers, it is important that we understand the selective effects that these changes in population density will have. As an example, there is increasing evidence that strong sexual selection can increase the risk of extinction (Doherty et al., 2003; Kokko & Brooks, 2003; Kokko & Rankin, 2006), at least in some taxa (Morrow & Fricke, 2004), but theoretical studies have shown that if there are density dependent changes in the strength or the direction of selection the risk of extinction is reduced (Rankin, 2007). Density-dependent selection for aggression might also feed back into population dynamics: it has been proposed that cycles in the population densities of small mammals in Canada (Krebs et al., 1973) and red grouse in Northern Britain (Watson et al., 1994) could be driven by selection for more aggressive males at high densities: these ideas have been unfashionable for some

years but new evidence has recently emerged to support them (Mougeot et al., 2003).

Background theory

Population density has long been thought of as being potentially important in determining the strength of intrasexual competition (Emlen & Oring, 1977; Kokko & Rankin, 2006) because as density increases the rate at which an animal makes contact with both competitors and potential mates is likely to increase. If males are competing for access to females, this increased contact rate is likely to lead to increased reproductive skew within the male population (Kokko & Rankin, 2006). As an example, consider a harem-defence polygyny system with males fighting for control of groups of females. As population density increases, so the number of opportunities for a male to add females to his harem will increase, as will the number of encounters with rival males. Thus, as density increases there will be more opportunities for the males that are most successful in contests to monopolize the available females, and so, other things being equal, reproductive skew within the male population should also increase.

This leads us to the question of what the optimal response of individual males to increasing densities of rivals and of potential mates should be. Intuitively, we expect increasing densities to lead to increasing amounts of aggression, but this is a consequence of our own experience of human behaviour and tells us little about how the fitness benefits and costs of different strategies will change with changing population density. A number of authors have argued that increasing density should select for more aggressive males (Zeh, 1987; Tomkins & Brown, 2004; Bertin & Cézilly, 2005), but others have argued the opposite, that at high densities aggressive males will be unable to defend females because of the large numbers of rival males present (Otte & Joern, 1975; Emlen & Oring, 1977; Borgia, 1980; Alcock & O'Neill, 1986; Connor, 1989; Rutowski, 1991; Clutton-Brock, Deutsch & Nefdt, 1993; Mills & Reynolds, 2003; Moczek, 2003). At first sight these ideas seem contradictory, but in fact they can be reconciled if we consider changes in the fitness of aggressive males across a broad range of densities (Ghiselin, 1974; Murray, 1987; Kwiatkowski & Sullivan, 2002; Pomfret & Knell, 2008), as shown schematically in Fig. 1. At low densities the fitness benefits from aggression will be small, and males that invest more in traits such as those used to locate females will be selected. As density increases so competition between males will become more intense (Kokko & Rankin, 2006), and at intermediate population densities this is likely to favour males who compete more aggressively: the costs of aggression will be outweighed by the benefits in terms of increased access to females. At high population densities, however, the costs of aggression may be greater than the benefits: firstly, a combative male will spend much of his time in contests with other males, and will pay high fitness costs from energetic expenditure and possibly injury (Jirotkul, 1999a; Kwiat-
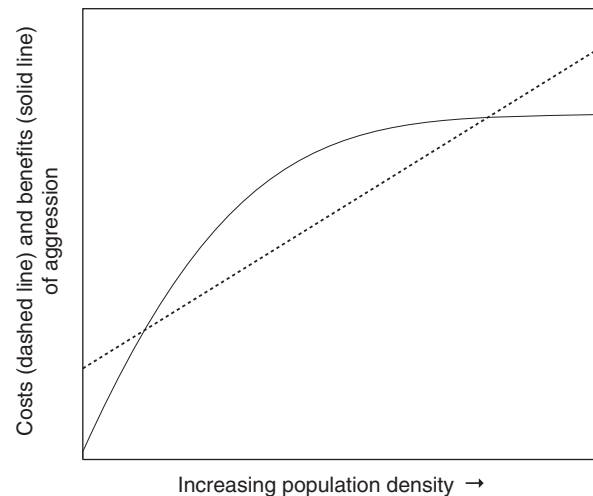

Figure 1 Hypothetical changes in the fitness benefits and costs of aggression as density increases. The broken line represents the costs of aggression, which in this case are assumed to increase linearly with density as contests become more frequent. The solid line shows the possible fitness benefits of aggression. At low densities the benefits are small because males are unlikely to encounter each other, and higher fitness will be achieved by investing in traits that enable males to locate receptive females. At high densities the benefits will reach a plateau and may even decrease because of effects like strong sperm competition, while the costs will continue to increase. Only at intermediate population densities, when the benefits of aggression are greater than the costs, will aggressive males be selected for.

kowski & Sullivan, 2002; Pomfret & Knell, 2008), secondly if resources are depleted at high population densities these costs of aggression may well be exacerbated (Moorcroft et al., 1996), and finally at high densities the fitness benefits per mating will be reduced if the number of matings per female increases as competition tends towards a 'scramble' model (Murray, 1987). Under these circumstances it may be the case that males who adopt less aggressive strategies and instead invest in traits that enhance their ability to move quickly between mates, or in traits associated with sperm competition, will have the highest fitness (Pomfret & Knell, 2008).

If these ideas are correct increases in population density can lead to selection for more or for less aggressive males, depending on how dense the initial population was. By the same token, and counter-intuitively, in some cases decreases in population density could lead to selection for more aggressive behaviour. Clearly, a better understanding of the circumstances under which these different results of population change might be expected would be very useful for predicting the effects of increases or decreases in the population sizes of species of conservation interest, for example. In this paper, I review the published literature on the relationship between population density and selection for aggression, firstly in order to assess whether population density is indeed an important force selecting for differing levels of aggression, secondly to try to understand how population density affects aggressive behaviour and thirdly to produce recommendations for future work.

Published data on density and aggression

Table 1 presents a summary of the published studies of the fitness benefits of intrasexual aggression in relation to population density that I have been able to identify by a combination of literature searches using Web of Knowledge and by following references made in other published papers. I have only included studies where the aggressive behaviour is specifically associated with mating success, and where fitness, selection or some proxy thereof has been measured: thus I have excluded studies that have described changes in behaviour with density if there is no measure of the fitness consequences of the change in behaviour. While the results from these latter studies can be suggestive of a change in selection, it is not possible to draw firm conclusions about selection from them (and of course, most of them were not carried out for this purpose). For a specific species behaviour is not necessarily shaped by selection at unusually high or low densities, and animals might not be plastic enough in their responses to density to behave optimally at all densities, so effects such as 'pathological' increases in aggression at high densities might occur.

In total, I have identified 13 studies, with the majority being of arthropods and with fish and mammals each being represented once. This bias probably reflects the relative ease of conducting such studies in arthropods. There is a diverse range of study types: in addition to simple measures like the relationship between weapon size and mating success at different densities (Connor, 1989) there are studies ranging from measurements of the proportion of 'fighter' morphs that develop at different densities in the case of the mite *Sancassiana berlesei* (Radwan, 1993*b*; Radwan, Unrug & Tomkins, 2002; Tomkins *et al.*, 2004) to interspecific studies investigating the relationships between density and weaponry between species (Zeh, 1987; Pomfret & Knell, 2008).

This diversity of studies in Table 1 means that it would be hard to carry out evaluations such as meta-analysis. Nonetheless, insights can be gained from an examination of this collection of work. Firstly, all of these papers report an effect of density on the fitness consequences of aggression. Secondly, and importantly, both increases and decreases in selection for aggression are reported. Seven studies found that increasing density selected against aggressive behaviour or some indicator thereof, whereas four found that aggressive behaviour appeared to be selected for at higher densities, and one study reported mixed results (Jann, Blanckenhorn & Ward, 2000). There are no reports of no effect. Whether this is because of a genuine rarity of negative results or because of publication bias is not known.

As mentioned above, the methods used in these studies varies widely. The simplest are those where the mating success of aggressive versus non-aggressive males have been compared at differing densities, either in the laboratory (Zeh, 1987; Bertin & Cézilly, 2005) or in the field (Warner & Hoffman, 1980; Connor, 1989). The two laboratory studies reported increases in mating success with body size (an indicator of fighting ability) in the isopod *Asellus aquaticus* and with chela size (i.e. weapon size) in the pseudoscorpion *Dinocheirus arizonensis* at higher densities. By contrast the two field studies found that mating success decreased at higher densities for territorial bluehead wrasse *Thalassoma bifasciatum* (Warner & Hoffman, 1980), and that horn length was only correlated with mating success in the forked fungus beetle *Bolitotherus cornutus* in low-density populations (Connor, 1989). Two further studies (Mclain, 1992; Jann *et al.*, 2000) have used field observations of mating rate to estimate the selection intensity operating on male body size at differing densities. In both cases body size is an important predictor of victory in contests, and so this provides an estimate of the strength of selection arising from intrasexual aggression. In one case (Mclain, 1992) selection for large body size was much stronger in lower density patches, and in the other (Jann *et al.*, 2000), a study of yellow dungflies *Scatophaga stercoraria*, sexual selection on male body size increased with density, but in one season with very high density this relationship did not hold at the highest densities, and the strength of selection on body size may even have declined at the very highest densities: the authors described the relationship as 'asymptotic' but the fitted quadratic model clearly shows a decline at densities greater than roughly 250 flies per pat.

A second group of studies has used the existence of species with dimorphic males, one morph with large weaponry that follows an aggressive strategy and one 'sneaker' morph with reduced or no weaponry, to investigate the selective advantages of aggression at different population densities. These dimorphisms are thought to arise when males adopt a conditional ESS, with individuals of different 'status' (generally this means the ability to win contests), adopting different strategies depending on which gives the greatest fitness and a threshold or switchpoint arising at the point where two strategies provide equal fitness (Gross, 1996). The position of this switchpoint in populations characterized by different densities can therefore provide information about how selection favours different behaviours as density changes.

Most of these studies have been conducted in arthropods: firstly, in the mite *S. berlesei* males only develop into armed 'fighter' males with the third pair of legs modified into weaponry in low density cultures, suggesting that at high densities this strategy brings no selective advantage (Timms, Ferro & Waller, 1980; Radwan, 1993*a*). Further research into this system showed that at intermediate densities only the larger males develop weaponry, and also demonstrated a cost of weaponry: a fighter morph eclosing from a tritonymph of a given size has a smaller body than a non-fighter 'scrambler' morph (Radwan *et al.*, 2002). A second example is the dung beetle *Onthophagus taurus*. This has been introduced into both the USA and Australia, and a comparison of populations in the USA and Eastern and Western Australia has found that the proportion of horned 'major' males is now lowest in the highest density populations (Moczek, 2003). Thirdly, Tomkins & Brown (2004) surveyed earwigs *Forficula auricularia* on island populations off

Table 1 Summary of published research to date on population density and selection for male intrasexual aggression

Species	Mating system	Type of study	Effect of increased density on fitness of aggressive males	References
Isopod *Asellus aquaticus*	Precopulatory guarding of individual females	Lab manipulation	*Increase*: body size (ability to take over mated pairs) predicts mating success at high density, antenna length (searching ability) predicts mating success at low density.	Bertin & Cézilly (2005)
Mite *Sancassiana berlesei*	Males guard groups of females	Lab manipulation of rearing density	*Decrease*: fewer 'fighter' morphs develop	Radwan (1993*a*,*b*) (see also Timms *et al.* (1980)
Pseudoscorpion *Dinocheirus arizonensis*	Males fight for access to receptive females	Lab manipulation	*Increase*: males with large chelae more successful	Zeh (1987)
Pseudoscorpions, 10 genera and 51 species within the Chernetidae	Males fight for access to receptive females	Interspecies comparison	*Increase*: sexual dimorphism in chela size correlated with density	Zeh (1987)
Earwig *Forficula auricularia*	Males fight for access to females, plus postcopulatory mate guarding	Comparison between island populations	*Increase*: more 'fighter' morphs present on higher density islands	Tomkins & Brown (2004)
Lygaeid seed bug *Neacoryphus bicrucis*	Males defend territories	Field observations of behaviour and mating used to calculate selection	*Decrease*: at low densities the larger males have a mating advantage that is reduced at the higher densities. Territoriality breaks down at high densities and males are likely to share plants.	Mclain (1992)
Dung beetle *Onthophagus Taurus*	Males guard females in tunnels	Comparison between introduced populations	*Decrease*: fewer 'fighter' morphs develop	Moczek (2003)
Onthophagine beetles (14 species)	Males guard females in tunnels	Interspecies comparison	*Decrease*: high density (more crowded) species are hornless	Pomfret & Knell (2008)
Forked fungus beetle *Bolitotherus cornutus*	Males fight for control of oviposition sites	Field observations	*Decrease*: horn length only correlated with mating success at low densities	Connor (1989)
Fig wasps (28 species)	Lethal combat between males within figs	interspecies comparison	*Decrease*: lethal combat is common only in species with few males per synconium	Reinhold (2003)
Yellow dung fly *Scathophaga stercoraria*	Postcopulatory guarding of mated females	Field observations plus laboratory measures of clutch size: fitness calculated from these data	*Mixed*: selection on male body size increased with density, but only at low to intermediate densities	Jann *et al.* (2000)
Bluehead wrasse *Thalassoma bifasciatum*	Males defend territories	Field observations	*Decrease*: large territorial males less successful	Warner & Hoffman (1980)
Soay sheep *Ovis aries*	Males compete aggressively for matings	Field observations	*Decrease*: less aggressive 'scurred' males with small horns have better survival at high population densities	Moorcroft *et al.* (1996)

the British mainland. Males of this species show a similar dimorphism to the examples discussed above, with so-called 'macrolabic' males growing large forceps and smaller forceps developing on the other morph, the 'brachylabic' males. Populations on different islands varied substantially in the proportion of males developing into each morph, and

the only variable that predicted this variation was population density on each island: islands with more earwigs also had a greater proportion of the more heavily armed macrolabic males.

Finally, a study of a dimorphic mammal has also yielded some interesting insights into the relationship between

population density and aggression. Soay sheep *Ovis aries* on the island of St Kilda exhibit a stable polymorphism for horn length, with around 12% of males and 24% of females carrying reduced 'scurred' horns. Scurred males do not compete for matings by contests with other males, but seek out unguarded females. The population of sheep on the island fluctuates because of periodic crashes, and it has been shown that although scurred males experience reduced mating success they have substantially better overwintering survival than males with large horns, but only when population densities are high (Moorcroft *et al*., 1996; Robinson *et al*., 2006).

At an interspecific level, two studies have compared investment in weaponry between species that are found at different densities. Zeh (1987) analysed published data on the size of the chelae of chernetid pseudoscorpions, and found that species that were caught in larger numbers tended to have larger chelae, suggesting selection for increased investment in weaponry at high densities. Secondly Pomfret & Knell (2008) recently examined the effects of density (quantified as mean crowding, (Lloyd, 1967)) and OSR on the presence or absence of weapons (horns) in a community of South African dung beetles from the tribe Onthophagini. Using an analysis that controlled for phylogeny it was found that horned species experienced less crowding and tended to have an even or slightly male-biased OSR, whereas hornless species all had female-biased sex ratios and experienced more crowding because of high population densities. A final study which did not control for phylogeny compared the incidence of injury in male fig wasps between 28 species that varied in the number of males present per synconium, and found that evidence of lethal combat was restricted to those species with few males per synconium (Reinhold, 2003).

Discussion

The chief finding of this review is that population density does affect selection for aggression, and that this effect can operate in either direction, with declines in aggression being reported roughly as often as increases. Why do we find such different results from different systems? As discussed earlier, both increases and decreases in aggression can be predicted from theory as density increases (Fig. 1), and many of the studies discussed above are at least consistent with this scheme: the study of *Asellus aquaticus* by (Bertin & Cézilly, 2005), for example, showed not only that body size, a proxy for fighting ability, determined mating success at high density, but also that antenna length, an indication of a male's ability to locate a mate, determined mating success at low density. Nonetheless, strong evidence to support this model is still lacking: in only one case (Jann *et al*., 2000) is there evidence that selection for aggression is strongest at intermediate densities, and as discussed above this pattern was only found in one field season out of four, and the authors interpreted it as a plateau at high densities rather than a decline. Some further evidence of humped relationships between aggression and density come from two studies

of behaviour that found that males are most likely to be aggressive or that fights between males are more severe at intermediate densities (Murray, 1987; Jirotkul, 1999*b*), but these must be interpreted cautiously in this context because of the difficulty in making inferences about selection from studies that have only measured behaviour.

One problem with assessing the strength of evidence for the model shown in Fig. 1 is that it is very difficult to compare densities between species because the effect of density will scale very differently in different systems. There may also be a 'file drawer' effect in that studies that have focussed on a range of densities that correspond to the region of inflexion in the fitness–density relationship for aggression will be much more likely to return a null result. Future work on this question must make a point of measuring fitness or selection across as broad a range of densities as possible in order to maximize the power of a study to test this model properly.

One example that apparently deviates from the expected pattern is the earwigs studied by Tomkins & Brown (2004): the islands with the highest proportion of macrolabic males (i.e. islands were animals with large weapons were most common) had extremely dense populations indeed (J. Tomkins, pers. comm.) and there is no suggestion of a reduction in selection for aggression at these very high densities. In this case, it seems that even as density approaches the highest values aggression continues to lead to increasing fitness benefits. Why should this be the case in this species but not in those other examples where the benefits of aggression seem to decline at high densities? It is likely that the reasons behind these differences between species in their responses to population density lie in the specific details of their biology, especially the costs and aggression and the mating system, and of their ecology, in particular the effects of high densities and the nature of their habitats.

Costs of aggression and mating system effects

The graph shown in Fig. 1 assumes that the costs of aggression increase with density, while the benefits increase to a plateau and could even decrease above a certain density. The actual relationship between density and the costs and benefits of aggression will of course vary between species. Different kinds of aggressive behaviour will have different costs: a ritualized contest between males that is settled quickly and carries little risk of injury clearly has lower costs than lethal combat that usually leads to the death of the loser, or than contests that require prolonged exertion or display. In species where combat is resolved by the use of weaponry there will be a cost associated with the possession of the weapon, and this cost will vary depending on factors such as the size and weight of the armament in question. In general, the more costly the weaponry the higher the intercept of the relationship between total cost and population density will be, and the greater the mean cost of aggression per contest, the steeper will be the slope. An increase in either the intercept or the slope of this line will lead to the

costs of aggression becoming greater than the benefits at a lower population density.

The most costly form of combat occurs when males kill each other, and in these cases any increase in density might lead to selection against aggression. Reinhold (2003) modelled the fitness consequences of lethal combat in fig wasps, and found that the frequency of lethal fighting was negatively dependent on the number of competitors per fig. In this context we can note that combat in *S. berlesei* is often lethal, and that in this species armed morphs only develop at low population densities (Radwan, 1993*a*).

The selective benefits of pursuing an aggressive strategy will also vary between species depending on factors such as the mating system, the nature of reproduction and the patterns of sperm utilization under sperm competition, with aggression being favoured in systems where males can monopolize the reproductive output from one or more females. As an example, consider a polyandrous species where males guard females after mating, with semelparous reproduction and last male sperm precedence. In this case the last male to mate with a female before oviposition will fertilize her entire lifetime reproductive output, so the selective benefits of guarding a female who is ready to oviposit will be very high. By contrast, in a species that is also polyandrous but with iteroparous reproduction and sperm mixing a male would have to guard and mate with a female for her entire reproductive lifespan in order to achieve the same benefit, and even one mating with another male before guarding would reduce his fitness. We would expect that males in the former species would continue to guard females even at high population densities, while in the latter case the selective benefits of aggressively guarding the female at high densities would be low, and a higher fitness might be achieved by investing in traits that will enhance a male's sperm competition performance, such as testis size.

Interactions with other effects of density

It is not only the encounter rate with conspecifics that increases with population density. Interspecific competition for resources, infection, parasitism and predation can all increase with population density (Begon, Townsend & Harper, 2005). These will all tend to lead to a reduction in condition for the individuals within a population, thereby making the relative costs of aggression greater. The soay sheep example described above (Moorcroft *et al.*, 1996; Robinson *et al.*, 2006) demonstrates this: in years of low population density horned males that aggressively compete for matings are able to survive over winter, but in years of high population density these animals have a lower survival rate than the less aggressive 'scurred' males. Mortality in the high density years occurs because the standing crop of vegetation is depleted and it seems that males pursuing an aggressive strategy are paying some cost that reduces their ability to survive at these times.

Habitat effects and the ability of males to monopolize females

Ultimately, the selective benefit of aggression between males arises from the ability of aggressive males to monopolize females (Emlen & Oring, 1977). The nature of the habitat of the species in question, plus the species behavioural response to that environment, will play an important role in determining how effectively a male can do this. While there is little direct evidence of habitat effects on male monopolization of females, an example of differential fitness was provided by Łukasik, Radwan & Tomkins (2006), who measured survival of fighter and scrambler morphs of the mite *S. berlesei* in simple (Petri dishes with Plaster of Paris on the bottom) and complex (Petri dishes with 10 mm sections of drinking straw embedded in the plaster base) environments. In the more complex environments the scrambler morphs only had a higher mortality rate, apparently because they were less able to escape from the fighter morphs in the more confined spaces that they were encountering them in.

Future work

This review has demonstrated that population density can indeed play an important role in the evolution of intrasexual aggression. Our understanding of this subject remains limited, however: although there has been some theoretical treatment of population effects on mating system evolution in general (Eshel, 1979; Kokko & Rankin, 2006) there is a clear need for modelling studies to help us to understand how such factors as the extent of promiscuity, the nature of sperm competition and the costs of individual contests will interact to determine whether the fittest males will be aggressive defenders of females or passive searchers and scramblers. Empirical studies, while also limited are somewhat further advanced but in the absence of a good theoretical framework it is difficult for experimentalists and field biologists to produce useful and directed studies. To date those studies that have been undertaken have largely been limited to determining whether there is an effect of density at all: future work might shift towards trying to obtain a deeper understanding by asking whether altering conditions such as resource availability or aspects of a species' biology such as the degree of promiscuity or the ease of finding a mate can change the relationship between density and the fitness consequences of aggressive or passive strategies. There are obvious opportunities here for laboratory manipulations and selection experiments.

Acknowledgements

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