ANIMAL BEHAVIOUR, 2007, **74**, 1593–1599
doi:10.1016/j.anbehav.2006.12.025

COMMENTARY

Plasticity in antiparasite behaviours and its suggested role in invasion biology

DAVID P. HUGHES*† & SYLVIA CREMER*
*Centre for Social Evolution, Institute of Biology, Department of Population Biology,
University of Copenhagen
†Department of Biology, University of Oulu, Finland

*(Received 21 September 2006; initial acceptance 27 October 2006;
final acceptance 15 December 2006; published online 24 September 2007; MS. number: SC-1305)*

Keywords: defence; evolution of increased competitive ability; immunity; invasion biology; parasites; phenotypic plasticity; superorganism

Invasive species represent a considerable threat both to biodiversity and ecosystem functioning (Cox 2004), as well as a massive economic burden (Pimentel et al. 2005). It is becoming increasingly clear that understanding why certain species become pests when introduced into new ranges requires a range of theories and interacting approaches (Hochberg & Gotelli 2005). It is hypothesized that successful invaders outcompete native ones due to the evolution of increased competitive ability (EICA, Blossey & Nötzold 1995) following their introduction. Many factors could contribute to the EICA and one which has received significant attention is the strong release from enemies following entry into the new range, the enemy release hypothesis (Mitchell & Power 2003; Torchin et al. 2003; recently reviewed in Colautti et al. 2004; Prenter et al. 2004). That is, invasive species do better than native ones because they lose most of their predators, herbivores and parasites as a result of the introduction event. The enemies that do occur in the introduced range generally do not pose a similar threat (e.g. because they are not adapted to this new arrival). Consequently, resources normally used for defence can be diverted into growth and reproduction and this affords a competitive advantage over native species. Enemy release is not the sole determinant of the EICA because many exotic species have been introduced, presumably without their enemies, and they did not become invasive pests (Cappuccino & Carpenter 2005; Suarez et al. 2005). The release from enemies probably interacts with other factors such as how many times the invading species was released (propagule pressure, Lockwood et al. 2005) and the ecological characteristics of the introduced species (Suarez et al. 2005). Accepting the interrelated nature underpinning the probability of becoming a successful pest we return our focus to enemy release, in particular, its parasite release component.

Parasite release and the associated EICA hypothesis was recently discussed by Lee & Klasing (2004) who argued that for introduced vertebrates the loss of parasites should generally reduce the necessity of an immune system for the introduced species. The logic being that immunity is expensive and the saved resources could be redirected to growth and reproduction. However, a complete shutdown of immune functions is a risky strategy since some parasite challenges after introduction are also possible (from generalist parasites that could attack introduced species). In light of these different selection pressures: Lee & Klasing (2004) hypothesized that successful vertebrate invaders are likely to be those which do not use a costly systemic inflammatory response; but rather rely on antibody mediated immunity which the authors consider less costly.

The immune system is an important defence against parasites. However, it is the last line of defence in a series of barriers (behaviour, morphology, biochemistry and life history: Combes 2001; Rigby et al. 2002) and so we might more correctly consider it to be an ‘emergency service’ (Siva-Jothy et al. 2005). In terms of response time, of all the above defensive barriers, behaviour will display the highest sensitivity to environmental change (West-Eberhard 2003, page 180) such as enemy release following

Correspondence: D. P. Hughes, Institute of Biology, Department of Population Biology, University of Copenhagen, Universitetsparken 15, Building 12, DK-2100 Copenhagen, Denmark (email: dphughes@bi.ku.dk). S. Cremer is now at the Biology I, University of Regensburg, D-93040 Regensburg, Germany

0003−3472/07/$30.00/0

introduction. Here we will put forward the hypothesis that plasticity in antiparasite behaviour is a defining feature of successfully invading animals. Before formulating our hypothesis, however, we will review the evidence that behaviour is indeed an effective, though costly, defence mechanism against parasites.

The Diversity, Effectiveness and Cost of Antiparasite Behaviours in Animals

The ability of parasites to adaptively manipulate the behaviour of their hosts is a well-known phenomenon (Dawkins 1982; Moore 2002). Examining the extent, adaptive function and proximate mechanisms of the extended phenotype of parasites have been a vibrant field over the last 20 years and one that shows no sign of decreasing (Moore et al. 2005; Thomas et al. 2005a). In contrast, studies that examine how hosts, through adaptive changes in behaviour, reduce either the probability of infection or the costs of parasitism once infected are rare (Moore 2002, page 92).

There is a wide range of behaviours that are directed against sources of infection such as parasitized conspecifics or areas of high parasite numbers (e.g. latrines), or directly against the parasites themselves (to prevent parasite entry or retard parasite development once entry is achieved). All of these behaviours have one common feature, they reduce the probability of infection of either the individual itself or its kin. A thorough review and examination of the types of defensive behaviours have recently been completed (Moore 2002, chapter 4). The main categories are: moving away from infection, habitat shifting, adjusting posture, minimizing visibility to parasites, grooming/swatting (including tool use) and food choice (including self-medication). The latter example, self-medication, highlights the important fact that antiparasite behaviours can also serve to reduce the costs once infected, or to retard parasite development. It includes the ingestion of certain substances (usually plant secondary compounds; Lozano 1998) or movement to an area unfavourable to parasite development, for example hot or cold zones (Kluger et al. 1975; Muller & Schmid-Hempel 1993; Moore & Freehling 2002). Defence can be enacted either singly, as a dyad (e.g. mutual grooming, tail swishing), or as a group. In the latter case the group may be a selfish herd (e.g. bovines) or a family unit (e.g. social insects, primates).

Antiparasite behaviour can be very effective in reducing parasite loads. For example when mammals were prevented from grooming, their ectoparasite loads increased considerably: ×2, ×20 and ×60 for cats, mice and impala, respectively (Murray 1961; Mooring et al. 1996; Eckstein & Hart 2000a). 'Aggressive grooming' by Japanese scarab beetle larvae reduced nematode attacks by 60% (Gaugler et al. 1994), while weeding behaviour of leaf-cutting ants when tending their symbiotic crop fungus achieved a complete removal of a generalist and up to 59% removal of a specialist fungal parasite (Currie & Stuart 2001). Remarkably, the ants can discriminate between fungal spores of different pathogenicity and preferentially clean up the most threatening first (Little et al. 2005). In a vertebrate example the antiparasite behaviour was shown to be better than the acquired immune system in reducing infection (Karvonen et al. 2004).

The costs of antiparasite behaviours have seldom been assessed but, where it has been investigated, they have been shown to be high. For example, bats and cats (Eckstein & Hart 2000b; Giorgi et al. 2001) spend a considerable amount of time grooming and in the former case this was accompanied by a significant increase in oxygen consumption (Giorgi et al. 2001). Similarly, fly-swatting behaviour by howler monkeys accounted for 24% of their metabolic budgets (Dudley & Milton 1990). In other examples where costs have not been calculated it is reasonable to assume that the behaviour is energetically expensive. Examples include tool use by elephants to swat flies (Hart & Hart 1994), cooperative behaviour among social insects when quarantining either infected individuals or the parasites themselves (Jeanne 1979; Epsky & Capinera 1988; Neumann et al. 2001), nest guarding by wasps and birds to prevent parasitism (West-Eberhard 1969; Gamboa 1978; McRae 1996), or selective foraging for plant compounds by chimps and ants to combat gut parasites and bacteria present in the nest (Lozano 1998; Christe et al. 2003). To summarize, antiparasite behaviour is both effective in reducing parasites and costly to use. We require more studies that address the efficacy and cost of antiparasite behaviour (Moore 2002), but there is no a priori reason to assume that the cited examples (and those below) are not representative of other taxa.

Hypothesis: Plasticity in Antiparasite Behaviour is a Trait of Invasive Animals

In the preceding section we showed that antiparasite behaviour, though effective is costly to maintain. Given these two observations and the additional one that introduction into a new range is often without coevolved parasites (enemy release) we suggest that antiparasite behaviour has a role in understanding invasion biology. Specifically, we hypothesize that successful invaders plastically switch off defensive behaviours when introduced into a new range and by doing so save resources. This would provide a competitive advantage not only over native species but also with respect to other introduced species or populations that do not show such plasticity. It is important to stress that the plastic nature is a core component of our hypothesis because, as we will show later, not all animals can switch off antiparasite behaviours.

Plastic antiparasite behaviour should be more important than plasticity in any of the other four barriers to infection (morphology, biochemistry, life history and immune systems) because behaviour is the most flexible component of an organism's phenotype (Baldwin 1896; West-Eberhard 2003). In short, 'behavior is the evolutionary pacemaker' (Wilson 1975, page 13). Lee & Klasing (2004) suggested that successful invaders may be those that simply switch off expensive immune system components such as the systemic inflammatory response, and use a supposedly less costly antibody response. However, this switch is not applicable to invertebrates because they only have costly innate immunity (Poulsen et al. 2002; Armitage et al. 2003; Siva-Jothy et al. 2005; Sadd & Siva-Jothy 2006). Because of their costly innate immune system it is possible that behaviour may play a particularly strong role for invertebrates. Therefore, we suggest that successful invaders (vertebrates and invertebrates) may be those that display plastic antiparasite behaviours, and that such plasticity may be particularly relevant to invertebrate invaders.

Testing the Plastic Antiparasite Behaviour Hypothesis

A test of our hypothesis should come from a phylogenetically controlled comparison of antiparasite behaviour between introduced and native range animals; and between those species that become invasive and those that, though introduced, fail to become invasive. We could then test if plasticity was a key trait of successful pests. Unfortunately, the lack of attention given to antiparasite behaviours means that the data for such comparisons are not available. Our motivation is to promote such studies, similar to a recent empirical study in plants (Cappuccino & Carpenter 2005), and one in fish (Rehage et al. 2005); the latter study did not directly look at parasites but compared the behavioural reaction of two invasive and two related, noninvasive mosquitofish species to novel predators and competitors.

In the absence of either sources of data with which to test our hypothesis we will attempt to argue in two steps that it none the less has merit and is deserving of consideration. Our first step will be to show that antiparasite behaviour can, in the native range of animals, be expressed plastically. The second step will then emphasize that behavioural plasticity sensu lato is already a hallmark of successfully invading species. Additionally, because the absence of antiparasite behaviours in an invasive population, relative to a native one, may reflect selection against a costly trait in a parasite free habitat we will conclude this section by emphasizing the evolutionary context of behavioural plasticity.

Antiparasite behaviours can be plastic

Given the high cost of antiparasite behaviour it is not surprising that animals may, dependent on the degree of risk, modulate the amount of time spent engaged in antiparasite defence behaviour. For example, reed warblers display a high degree of behavioural plasticity in the face of brood parasitism by cuckoos and will quickly reduce behavioural defence (egg rejection) if parasite numbers decrease (Brooke et al. 1998). In intraspecific brood parasitism variation in defensive behaviours are also observed (McRae 1996). An exactly analogous situation occurs in ants (D'Ettorre et al. 2004) which switch off parasite recognition mechanisms when the brood parasite (also called a social parasite) is absent. Similarly, social wasp queens decide to engage in costly defence strategies that involve making alliances with other females when parasitism risk is high (Gamboa 1978, see similar example involving a moth where the cost is building a new nest, Jeanne 1979). Farming insects (ants that rear fungi as food) also protect occupants of the nest, their fungal crop, from parasitism and here the behaviours are plastic, effective and rapidly deployed (Currie & Stuart 2001; Little et al. 2005). Plasticity in antiparasite behaviour also occurs at the individual level. In self-medicating baboons that ingest plants to combat gut parasites the natural exclusion of the parasite by a waterfall (*Schistosoma* spp. using a snail host) is enough to reduce the incidence of the defensive behaviour (reviewed along with chimp examples in Lozano 1998). Individual ants are plastic in their response to parasitoid flies (Feener 1981; Orr et al. 1995). Plasticity in the expression of antiparasite behaviour does not just change only with varying parasite pressure but can also be influenced by individual condition. In sheep the expression of antiparasite behaviour is contingent on present infection status (Hutchings et al. 1998) and reproductive state (Hutchings et al. 2002). Humans are believed to have evolved antiparasite behaviour which are manifested as avoidance of strangers (xenophobia) and disabled individuals (the logic being it is an outward sign of a disease such as polio): similar to sheep our responses vary according to our perceived infection status (Park et al. 2003; Faulkner et al. 2004) or reproductive status (Curtis et al. 2004; Jones et al. 2005; Navarrete et al. 2007). All the above examples show that plasticity in antiparasite behaviour occurs in the native range of animals and so should also occur if animals are transplanted to new ranges as happens in species invasions. For our hypothesis, which suggests that plasticity in antiparasite behaviour is a defining trait of successful invasive species, it is necessary to find examples where introduced species maintain expensive antiparasite behaviour in the absence of parasites.

Studies have not addressed antiparasite behaviour of introduced animals when accidentally introduced into new ranges. As a proxy though we may examine one human mediated transplantation experiment which regularly occurs. That is, the placement of animals in artificial habitats such as zoos, animal research facilities and human homes. Ungulates, felids and rodents in artificial environments where parasite pressure is low or absent still perform grooming behaviour (Eckstein & Hart 2000a, b; Mooring et al. 2004). Unless grooming has a secondary role than just parasite removal (e.g. social bonding in primates) then its maintenance in the absence of parasites requires explanation. Adopting the terminology of researchers examining grooming behaviour one explanation for its persistence is that grooming is a 'programmed action' than a 'stimulus driven response' (Hart et al. 1992). Those groups that belong to the latter category, which requires an elicitator such as a parasite, may possess more plasticity in their antiparasite behaviour and could possibly be superior invaders in line with our hypothesis.

The expression of antiparasite behaviour when parasites are absent would be maladaptive. Similarly, behavioural defence against parasites that do not pose an infection risk would also be maladaptive. We do know some groups can recognize infective agents preferentially, ants for example clean up infective fungal spores, but not if they have been irradiated and rendered noninfective (Little et al. 2005).

Behavioural defence against noninfective parasites would be especially relevant in the introduced range because it would be full of parasites that were not coevolved with the introduced species. Examples of this are rare and probably difficult to prove but one possibility is the defensive behaviour of wasps to noninfective stage parasitic insects (i.e. male strepsipterans: Hubbard 1892; D. P. Hughes, personal observation) which resembles the adaptive antiparasite behaviour of wasps to infective parasitic insects (ovipositing female ichneumonid wasps: West-Eberhard 1969, personal communication). Since relatively little research has focused on antiparasite behaviours, other examples of its expression in the absence of parasites may have gone unnoticed.

Behavioural plasticity in invasion biology

We will now highlight examples where behavioural plasticity, sensu lato plays a role in the success of invasive species. Until recently very little work has focused on the role of behaviour in invasion biology so a review of the literature, or meta-analysis, is premature. We will confine our examples to birds and ants because these are the animal taxa for which we have the greatest understanding of the invasion process following two key publications (Sol et al. 2005; Suarez et al. 2005).

Big brains among invasive birds give them an advantage in ranges into which they have been introduced (Sol et al. 2005). Examining a database of more than 600 introductions, Sol et al. (2005) showed that relative to body size, birds with larger brains tend to be more successful in establishing themselves in novel environments. The reason appears to be related to an 'innovation propensity' (Sol et al. 2005) meaning larger brained birds would be more likely to engage in novel actions. A prime example is accepting new food items that have not previously been encountered (see recent empirical evidence by Martin & Fitzgerald 2005). Such behavioural plasticity is likely to be a preadaptation for invasiveness and probably reflects environmental variation present in the native range of the species (Mason & Reidinger 1982).

Ants are not known for their big brains, but concurrent performance of behaviour means colonies as a whole can display behaviour not possible by individuals: the whole is greater than the sum of its parts (Oster & Wilson 1978; Hölldobler & Wilson 1990; Anderson et al. 2002). Colonies can therefore be seen as an integrated unit, or 'superorganism' (Wheeler 1911; Wilson 1985; Bourke & Franks 1995). Heuristically, we can think of this superorganism having a 'social brain' which shows plasticity in behavioural expression. Such plasticity has already been recognized to be important in the success of some invasive social insects. For example, a major determinant in the success of invading ants, with the Argentine ant as the best studied example, has been the loss of territorial aggression against conspecific colonies (Passera 1994; Holway & Suarez 1999). This has been likened to successful strategies underlying human empire expansion ('Pax Argentinica': Queller 2000). Not expending energy in intercolony aggression frees resources for growth and reproduction (Holway et al. 1998) and gives enormous advantages in interspecific competition (Holway et al. 2002). Aggression levels displayed by invasive ants depend on the genetic composition of the group (Tsutsui et al. 2003) but are not fixed, that is, aggression increases when workers of the same two colonies encounter repeatedly (Thomas et al. 2005b). Therefore, aggression levels of invasive ants are highly plastic and change even within short time frames.

Another example of superorganism plasticity is where to build the nest. Successful invasive ants are mostly ground nesting and the more specialized arboreal nesters do not become invasive despite being released many times (Suarez et al. 2005). Of the 81 species of arboreal ant released into mainland U.S.A. between 1927 and 1985 only four have become successful invaders. Importantly, in their native range all four 'show considerable flexibility in their choice of nesting sites' (Suarez et al. 2005).

The limited available examples of behavioural plasticity among successfully invading birds and ants suggest that behavioural plasticity may be important in invasion biology. As Baldwin (1896) phrased it, behavioural plasticity allows a species 'to rise to the occasion'. It does not necessarily follow that plasticity in those traits mentioned (food choice, nest defence and nest location) means plasticity occurs in antiparasite behaviour as well. But likewise there is no reason not to suspect an association. The notion of modularity in phenotypic plasticity would argue against interconnectedness, but as West-Eberhard (2003, page 81) pointed out, the modularity concept should not be pushed to its extreme for fear of becoming useless. Besides, our hypothesis is not constructed on a base that some pests have plasticity in diverse behaviours and ergo must have plasticity in antiparasite behaviour. Rather, the foundation of our theory is that antiparasite behaviour is expensive but effective and occasionally plastic: in the absence of enemies those that plastically switch off such behaviours will have an advantage. We have so far argued that plasticity in antiparasite behaviour can give introduced species an advantage over ecological timescales. However, when plasticity is heritable, which in the next paragraph we discuss can be the case, selection in the new range will favour these plastic genotypes over genotypes that cannot plastically adapt to the environmental changes. The evolutionary context of behavioural plasticity is also relevant.

The evolutionary context of plasticity

Recent evidence from a long-term study of breeding behaviour in great tits has highlighted the heritability of phenotypic plasticity (Nussey et al. 2005). Breeding birds displayed considerable genetic variation in phenotypic plasticity (when to breed) and following significant environmental changes selection has acted upon this. Any test of the plastic antiparasite behaviour hypothesis should be aware of the role of heritability in phenotypic plasticity. That is, in addition to the ecological context which we have hitherto discussed, the evolutionary timescale is relevant. In the new habitat the most plastic genotypes might be selected for, especially if multiple introductions from the native range source population continue to introduce individuals with varying degrees of phenotypic plasticity. Alternatively, since plasticity is assumed to be expensive (Pigliucci 2001), selection might favour genotypes that have lost their plasticity. Furthermore, if genes drive behavioural plasticity then the genetic bottlenecks which introduced species typically pass through during introduction may reduce genetic diversity and a concomitant decrease in the plasticity of behaviours might be observed. In addition to any selection on phenotypic plasticity there could be selection on antiparasite behaviour itself. For example, if populations have, for a considerable period of time been in an environment that is free of their own specialized parasites (such as an introduced range) then an absence of antiparasite behaviour (relative to populations in the native range) may reflect selection against costly antiparasite behaviours. Note that the introduced range lacks the specialized parasites of the introduced species and not parasites in general which will be present. To conclude, even if the plasticity in antiparasite behaviours should be clearly favoured over ecological timescales, the effect of long-term selection on invasive species in their introduced range is far from clear.

Conclusions

Unfortunately there will be no single solution to the ever escalating problem of invasive species and it is becoming increasingly clear that invasion biology is not a predictive science (Hochberg & Gotelli 2005). The greatest chance of success for ameliorating the costs is an appreciation of many diverse factors involved: from international trade agreements and corporate accountability (Simberloff 2005) to the number of release events and size of propagules (Lockwood et al. 2005). Here we sought to integrate behaviour, invasion biology and immunity in an attempt to bring about an increased focus on the role of antiparasite behaviour in invasion biology.

Before closing it is important stress that not all host–parasite interactions are equal and this of course reflects the enormous biodiversity of parasites themselves (Poulin & Morand 2000). Space has not allowed us to discuss our hypothesis with respect to diverse parasite taxa but it is worth stating that antiparasite behaviour may be irrelevant in a number of host-parasite interactions and, as always, an appreciation of natural history and life histories is vital. The latter point simply mirrors a recent opinion that too often the natural history of the invading species themselves is unknown (Suarez et al. 2005). Invasion biology must function with a thorough understanding of the natural history of the invading organisms in the introduced and native ranges if control programs are ever to succeed.

In conclusion, we put forward the suggestion that plastic antiparasite behaviour has a role in invasion biology. Behavioural defence is effective in reducing parasitism though costly to maintain. It can be maladaptive under scenarios of parasite release and successful invaders may be those that reduce these high costs via behavioural plasticity; that is, only applying behavioural defence when it is required. Further efforts are needed to examine this important component of parasite defence in both native and introduced ranges. Such work may identify taxa that are likely to be successful invaders; as well as facilitating the development of ‘evolutionary enlightened management’ practices (Schlaepfer et al. 2005). These steps should be taken with full appreciation of other important determinants of invasion success to more effectively tackle what is a highly serious threat.

We thank Janice Moore, Jacobus J. Boomsma and Michl Sixt for comments on the manuscript. We are grateful for comments of the two editors, Leigh W. Simmons and Louise Barrett as well as three anonymous referees; in particular one who drew our attention to the relevance of the evolutionary context of phenotypic plasticity. This work has also benefited greatly from discussions with Andy Dobson, Peter Hudson, Carlos Navarette, Mark Schaller, Mike Siva-Jothy and Mary Jane West-Eberhard. Financial support was given by the European Commission (Research Training Network, INSECTS, established under the Improving Human Potential Programme to the Universities Oulu and Copenhagen (contract HPRN-CT-2000-00052); and two Marie Curie Individual Intra-European Fellowships in the Framework Program 6 (MEIF-CT-2003-501766 to S.C. and MEIF-CT-2006-041613 D.P.H.).

References

Anderson, C., Theraulaz, G. & Deneubourg, J. L. 2002. Self-assemblages in insect societies. *Insectes Sociaux*, **49**, 99–110.

Armitage, S. A. O., Thompson, J. J. W., Rolff, J. & Siva-Jothy, M. T. 2003. Examining costs of induced and constitutive immune investment in *Tenebrio molitor*. *Journal of Evolutionary Biology*, **16**, 1038–1044.

Baldwin, J. M. 1896. A new factor in evolution. *American Naturalist*, **30**, 441–451 536–553.

Blossey, B. & Nötzold, R. 1995. Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887–889.

Bourke, A. F. G. & Franks, N. R. 1995. *Social Evolution in Ants*. Princeton, New Jersey: Princeton University Press.

Brooke, M. D., Davies, N. B. & Noble, D. G. 1998. Rapid decline of host defences in response to reduced cuckoo parasitism: behavioural flexibility of reed warblers in a changing world. *Proceedings of the Royal Society of London, Series B*, **265**, 1277–1282.

Cappuccino, N. & Carpenter, D. 2005. Invasive exotic plants suffer less herbivory than non-invasive exotic plants. *Biology Letters*, **1**, 435–438.

Christe, P., Oppliger, A., Bancala, F., Castella, G. & Chapuisat, M. 2003. Evidence for collective medication in ants. *Ecology Letters*, **6**, 19–22.

Colautti, R. I., Ricciardi, A., Grigorovich, I. A. & MacIssac, H. J. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters*, **7**, 721–723.

Combes, C. 2001. *Parasitism: the Ecology and Evolution of Intimate Interactions*. Chicago, Illinois: University of Chicago Press.

Cox, G. W. 2004. *Alien Species and Evolution: the Evolutionary Ecology of Exotic Plants, Animals, Microbes, and Interacting Native Species*. Washington, DC: Island Press.

Currie, C. R. & Stuart, A. E. 2001. Weeding and grooming of pathogens in agriculture by ants. *Proceedings of the Royal Society of London, Series B*, **268**, 1033–1039.

Curtis, V., Aunger, R. & Rabie, T. 2004. Evidence that disgust evolved to protect from risk of disease. *Proceedings of the Royal Society of London, Series B*, **271** (Supplement), 131–133.

Dawkins, R. 1982. *The Extended Phenotype*. Oxford: W.H. Freeman.

D'Ettorre, P., Brunner, E., Wenseleers, T. & Heinze, J. 2004. Knowing your enemies: seasonal dynamics of host—social parasite recognition. *Naturwissenschaften*, **91**, 594—597.

Dudley, R. & Milton, K. 1990. Parasite deterrence and the energetic costs of slapping in Howler monkeys, *Alouatta palliata*. *Journal of Mammalogy*, **71**, 463—465.

Eckstein, R. A. & Hart, B. L. 2000a. Grooming and control of fleas in cats. *Applied Animal Behaviour Science*, **68**, 141—150.

Eckstein, R. A. & Hart, B. L. 2000b. The organization and control of grooming in cats. *Applied Animal Behaviour Science*, **68**, 131—140.

Epsky, N. D. & Capinera, J. L. 1988. Efficacy of the entomogenous nematode *Steinernema feltiae* against a subterranean termite, *Reticulitermes tibialis* (Isoptera, Rhinotermitidae). *Journal of Economic Entomology*, **81**, 1313—1317.

Faulkner, J., Schaller, M., Park, J. H. & Duncan, L. A. 2004. Evolved disease-avoidance mechanisms and contemporary xenophobic attitudes. *Group Processes and Intergroup Relations*, **7**, 333—353.

Feener, D. H., Jr 1981. Competition between ant species: outcome controlled by parasitic flies. *Science*, **214**, 815—817.

Gamboa, G. J. 1978. Intraspecific defense: advantage of social cooperation among paper wasp foundresses. *Science*, **199**, 1463—1465.

Gaugler, R., Wang, Y. & Campbell, J. F. 1994. Aggressive and evasive behaviours in *Popillia japonica* (Coleoptera, Scarabaeidae) larvae defenses against entomopathogenic nematode attack. *Journal of Invertebrate Pathology*, **64**, 193—199.

Giorgi, M. S., Arlettaz, R., Christe, P. & Vogel, P. 2001. The energetic grooming costs imposed by a parasitic mite (*Spinturnix myoti*) upon its bat host (*Myotis myotis*). *Proceedings of the Royal Society of London, Series B*, **268**, 2071—2075.

Hart, B. L. & Hart, A. L. 1994. Fly switching by Asian elephants: tool use to control parasites. *Animal Behaviour*, **48**, 35—45.

Hart, B. L., Hart, L. A., Mooring, M. S. & Olubayo, R. 1992. Biological basis of grooming behaviour in antelope: the body size, vigilance and habitat principles. *Animal Behaviour*, **44**, 615—631.

Hochberg, M. E. & Gotelli, N. J. 2005. An invasions special issue. *Trends in Ecology & Evolution*, **20**, 211.

Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusetts: Harvard University Press.

Holway, D. A. & Suarez, A. V. 1999. Animal behaviour: an essential component of invasion biology. *Trends in Ecology & Evolution*, **14**, 328—330.

Holway, D. A., Suarez, A. V. & Case, T. J. 1998. Loss of intraspecific aggression in the success of a widespread invasive social insect. *Science*, **282**, 949—952.

Holway, D. A., Lach, L., Suarez, A. V., Tsutsui, N. D. & Case, T. J. 2002. The causes and consequences of ant invasions. *Annual Review of Ecology and Systematics*, **33**, 181—233.

Hubbard, H. G. 1892. The life history of *Xenos*. *Canadian Entomologist*, **24**, 257—261.

Hutchings, M. R., Kyriazakis, I., Anderson, D. H., Gordon, I. J. & Coop, R. L. 1998. Behavioural strategies used by parasitized and non-parasitized sheep to avoid ingestion of gastro-intestinal nematodes associated with faeces. *Animal Science*, **67**, 97—106.

Hutchings, M. R., Milner, J. M., Gordon, I. J., Kyriazakis, I. & Jackson, F. 2002. Grazing decisions of Soay sheep, *Ovis aries*, on St Kilda: a consequence of parasite distribution? *Oikos*, **96**, 235—244.

Jeanne, R. L. 1979. Construction and utilization of multiple combs in *Polistes canadensis* in relation to the biology of a predaceous moth. *Behavioral Ecology and Sociobiology*, **4**, 293—310.

Jones, B. C., Perrett, D. I., Little, A. C., Boothroyd, L., Cornwell, R. E., Feinberg, D. R., Tiddeman, B. P., Whiten, S., Pitman, R. M., Hillier, S. G., Burt, D. M., Stirrat, M. R., Law Smith, M. J. & Moore, F. R. 2005. Menstrual cycle, pregnancy and oral contraceptive use alter attraction to apparent health in faces. *Proceedings of the Royal Society of London, Series B*, **272**, 347—354.

Karvonen, A., Seppala, O. & Valtonen, E. T. 2004. Parasite resistance and avoidance behaviour in preventing eye fluke infections in fish. *Parasitology*, **129**, 159—164.

Kluger, M. J., Ringler, D. J. & Anver, M. R. 1975. Fever and survival. *Science*, **188**, 166—168.

Lee, K. A. & Klasing, K. C. 2004. A role for immunology in invasion biology. *Trends in Ecology & Evolution*, **19**, 523—529.

Little, A. E. F., Murakami, T., Mueller, U. G. & Currie, C. R. 2005. Defending against parasites: fungus-growing ants combine specialized behaviours and microbial symbionts to protect their fungus gardens. *Biology Letters*, **2**, 12—16.

Lockwood, J. L., Cassey, P. & Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223—228.

Lozano, G. A. 1998. Parasitic stress and self-medication in wild animals. In: *Stress and Behaviour, Advances in the Study of Behaviour* (Ed. by A. P. Moller, M. Milinski & P. J. B. Slater), pp. 291—317. London: Academic Press.

McRae, S. B. 1996. Brood parasitism in the moorhen: brief encounters between parasites and hosts and the significance of an evening laying hour. *Journal of Avian Biology*, **27**, 311—320.

Martin, L. B., II & Fitzgerald, L. 2005. A taste for novelty in invading house sparrows, *Passer domesticus*. *Behavioral Ecology*, **16**, 702—707.

Mason, J. R. & Reidinger, R. F. J. 1982. Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *Auk*, **99**, 548—554.

Mitchell, C. E. & Power, A. G. 2003. Release of invasive plants from fungal and viral pathogens. *Nature*, **421**, 625—627.

Moore, J. 2002. *Parasites and the Behaviour of Animals*. Oxford: Oxford University Press.

Moore, J. & Freehling, M. 2002. Cockroach hosts in thermal gradients suppress parasite development. *Oecologia*, **133**, 261—266.

Moore, J., Adamo, S. & Thomas, F. 2005. Manipulation: expansion of the paradigm. *Behavioural Processes*, **68**, 283—287.

Mooring, M. S., McKenzie, A. A. & Hart, B. L. 1996. Grooming in impala: role of oral grooming in removal of ticks and effects of ticks in increasing grooming rate. *Physiology and Behavior*, **59**, 965—971.

Mooring, M. S., Blumstein, D. T. & Stoner, C. J. 2004. The evolution of parasite-defence grooming in ungulates. *Biological Journal of the Linnean Society*, **81**, 17—37.

Muller, C. B. & Schmid-Hempel, P. 1993. Exploitation of cold temperature as defense against parasitoids in bumblebees. *Nature*, **363**, 65—67.

Murray, M. D. 1961. The ecology of the louse *Polyplax serrate* (burm.) on the mouse *Mus musculus* L. *Australian Journal of Zoology*, **9**, 1—11.

Navarrete, C. D., Fessler, D. M. T. & Eng, S. J. 2007. Elevated ethnocentrism in the first trimester of pregnancy. *Evolution and Human Behavior*, **28**, 60—65.

Neumann, P., Pirk, C. W. W., Hepburn, H. R., Solbrig, A. J., Ratnieks, F. L. W., Elzen, P. J. & Baxter, J. R. 2001. Social encapsulation of beetle parasites by Cape honeybee colonies (*Apis mellifera capensis* Esch.). *Naturwissenschaften*, **88**, 214—216.

Nussey, D. H., Postma, E., Gienapp, P. & Visser, M. 2005. Selection on heritable phenotypic plasticity in a wild bird population. *Science*, **310**, 304—306.

Orr, M. R., Seike, S. H., Benson, W. W. & Gilbert, L. E. 1995. Flies suppress fire ants. *Nature*, **373**, 292—293.

Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology in the Social Insects*. Princeton, New Jersey: Princeton University Press.

Park, J. H., Faulkner, J. & Schaller, M. 2003. Evolved disease-avoidance processes and contemporary anti-social behaviour:

prejudicial attitudes and avoidance of people with physical disabilities. *Journal of Nonverbal Behavior*, **27**, 65–87.

Passera, L. 1994. Characteristics of tramp species. In: *Exotic Ants: Biology, Impact, and Control of Introduced Species* (Ed. by D. F. Williams), pp. 23–43. Boulder, Colorado: Westview Press.

Pigliucci, M. 2001. *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, Maryland: John Hopkins University Press.

Pimentel, D., Zuniga, R. & Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics*, **52**, 273–288.

Poulin, R. & Morand, S. 2000. The diversity of parasites. *Quarterly Review of Biology*, **75**, 277–293.

Poulsen, M., Bot, A. N. M., Nielsen, M. G. & Boomsma, J. J. 2002. Experimental evidence for the costs and hygienic significance of the antibiotic metapleural gland secretion in leaf-cutting ants. *Behavioural Ecology and Sociobiology*, **52**, 151–157.

Prenter, J., MacNeil, C., Dick, J. T. A. & Dunn, A. M. 2004. Roles of parasites in animal invasions. *Trends in Ecology & Evolution*, **19**, 385–390.

Queller, D. C. 2000. Pax Argentinica. *Nature*, **405**, 519–520.

Rehage, J. C., Barnett, B. K. & Sih, A. 2005. Behavioral responses to a novel predator and competitor of invasive mosquitofish and their non-invasive relatives (*Gambusia* sp.). *Behavioral Ecology and Sociobiology*, **57**, 256–266.

Rigby, M. C., Hechinger, R. F. & Stevens, L. 2002. Why should parasite resistance be costly? *Trends in Parasitology*, **18**, 116–120.

Sadd, B. & Siva-Jothy, M. T. 2006. Self-harm caused by insect's innate immunity. *Proceedings of the Royal Society of London, Series B*, **273**, 2571–2574.

Schlaepfer, M. A., Sherman, P. W., Blossey, B. & Runge, M. C. 2005. Introduced species as evolutionary traps. *Ecology Letters*, **8**, 241–246.

Simberloff, D. 2005. The politics of assessing risk for biological invasions: the USA as a case study. *Trends in Ecology & Evolution*, **20**, 216–222.

Siva-Jothy, M., Moret, Y. & Rolff, J. 2005. Insect immunity: an evolutionary ecology perspective. *Advances in Insect Physiology*, **32**, 1–48.

Sol, D., Duncan, R. P., Blackburn, T. M., Cassey, P. & Lefebvre, L. 2005. Big brains, enhanced cognition, and response of birds to novel environments. *Proceedings of the National Academy of Sciences, U.S.A.* **102**, 5460–5465.

Suarez, A. V., Holway, D. A. & Ward, P. S. 2005. The role of opportunity in the unintentional introduction of nonnative ants. *Proceedings of the National Academy of Sciences, U.S.A.* **102**, 17032–17035.

Thomas, F., Adamo, S. & Moore, J. 2005a. Parasitic manipulation: where are we and where should we go? *Behavioural Processes*, **68**, 185–199.

Thomas, M. L., Tsutsui, N. D. & Holway, D. A. 2005b. Intraspecific competition influences the symmetry and intensity of aggression in the Argentine ant. *Behavioral Ecology*, **16**, 472–481.

Torchin, M. E., Lafferty, K. D., Dobson, A. P., McKenzie, V. J. & Kuris, A. M. 2003. Introduced species and their missing parasites. *Nature*, **421**, 628–630.

Tsutsui, N. D., Suarez, A. V. & Grosberg, R. K. 2003. Genetic diversity, asymmetrical aggression, and recognition in a widespread invasive species. *Proceedings of the National Academy of Sciences, U.S.A.* **100**, 1078–1083.

West-Eberhard, M. J. 1969. *The Social Biology of Polistine Wasps* Vol. 140. Miscellaneous Publications of the Museum of Zoology, University of Michigan pp. 1–101.

West-Eberhard, M. J. 2003. *Developmental Plasticity and Evolution*. New York: Oxford University Press.

Wheeler, W. M. 1911. The ant-colony as an organism. *Journal of Morphology*, **22**, 307–325.

Wilson, E. O. 1975. *Sociobiology: the New Synthesis*. Cambridge, Massachusetts: Harvard University Press.

Wilson, E. O. 1985. The sociogenesis of insect colonies. *Science*, **228**, 1489–1495.