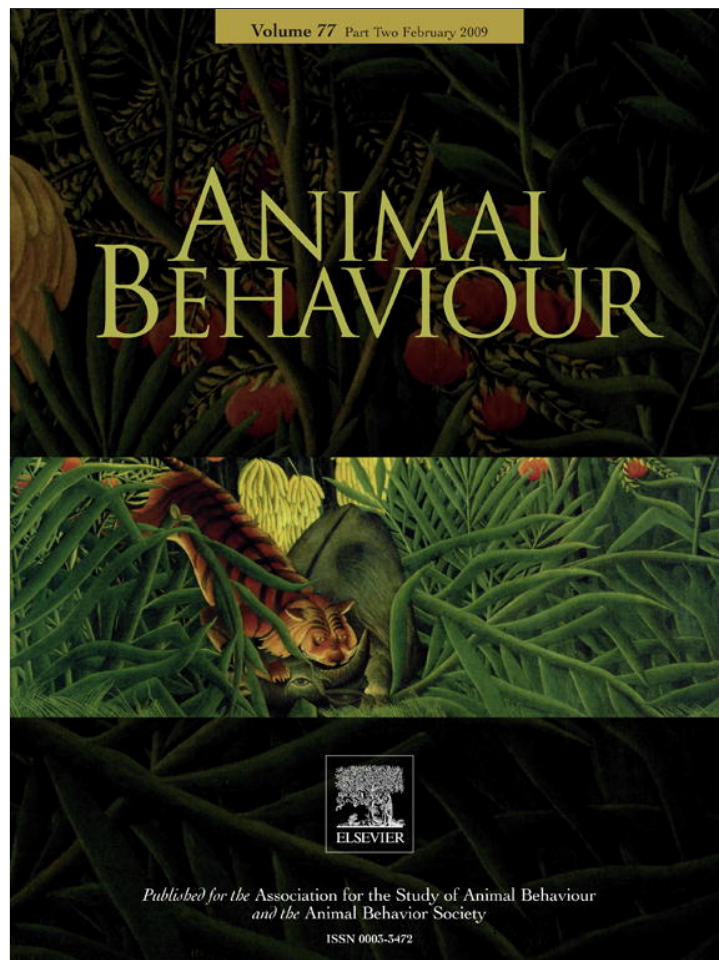


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To fight or not to fight: context-dependent interspecific aggression in competing ants

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Animals assess many factors when choosing how aggressively to behave during interspecific competitive interactions. Aggressive behaviour can help win resources, but it can also be costly. Here we tested how context such as competitor familiarity, habitat type and resource value affect competitive behaviour using two ant species, *Formica xerophila* and *F. integroides*. We found that competitive encounters within an individual's territory yielded more aggressive interactions than encounters in a neutral arena, and aggression towards competitors increased with resource value. Using a recently developed design combining behaviour assays between live ant dyads and ants paired with glass beads chemically resembling competitors, we isolated an individual's behaviour during an encounter to show that its behaviour can be significantly affected by the behaviour of its competitor during the interaction. Furthermore, we determined that context can affect each species differently, and that these differences are consistent with differences in overall fighting abilities. *Formica integroides* from trees (but not from nests) behaved differently towards live and artificial *F. xerophila*. *Formica integroides* are behaviourally dominant, which facilitates a strategy wherein individuals aggressively defend the nest but reciprocate the behaviours of their opponents (showing an interspecific Tit-for-Tat strategy) when defending less valuable locations. *Formica xerophila* are generally submissive, which favours a highly context-dependent strategy. In particular, *F. xerophila* discriminate between familiar and unfamiliar *F. integroides*, and behave more aggressively towards foreign competitors than towards neighbouring competitors. Differences between species' behaviours suggest that these interspecific interactions are dynamic context-dependent associations that cannot be reduced to a static dominance hierarchy.

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All animals must choose whether to avoid, tolerate or fight with competitors (King 1973; Schoener 1983). Although aggressive behaviour towards a competitor is sometimes necessary, aggression can be costly in terms of energy spent, time lost, and possible injury or mortality (Jaeger 1981; Cole 1986). Consequently, many theoretical and empirical studies have weighed the trade-off between costs and benefits of aggression (Maynard Smith & Price 1973; Axelrod & Hamilton 1981; Riechert 1998), finding actual or predicted behaviours ranging from absolute tolerance (Errard et al. 2003) to complete aggression (Provencher & Riechert 1995).

The optimal level of aggression towards a competitor can vary with the context of the interaction. For example, seasonal variation and/or reproductive cycle (Cristol & Johnsen 1994; Torkarz et al. 1998; Woodley & Moore 1999; Thurin & Aron 2008), food availability (Nicieza & Metcalfe 1997; Downs & Ratnieks 2000; Kim 2000), familiarity between competitors (Fisher 1954; Ydenberg et al. 1988; Temeles 1994), resource value (Robinson 1985; Reeve

1989), habitat type (Rodriguez 1995; Langkilde & Shine 2004) and disparity between contestants' fighting abilities (Maynard Smith 1979; Robinson 1985; Riechert 1998) have all been shown to affect competitive aggressive interactions for a variety of taxa.

Additionally, an animal's optimal behaviour in a contest may depend on its competitor's behaviour (Riechert 1998). For example, the Tit-for-Tat (TFT) strategy, in which a contestant initially cooperates (acts nonaggressively) with a competitor, then reciprocates the last action of its opponent during subsequent interactions, is an effective strategy in the iterated Prisoner's Dilemma (Axelrod & Hamilton 1981). Studies of context-dependent aggression that overlook one of the contestant's actions consequently risk misinterpreting key aspects of an encounter (discussed in Gravel et al. 2004). For example, aggression might be a response to a competitor's escalation; while tolerance might be a response to a competitor's avoidance or appeasement. Competitor behaviour could also have contradictory effects on a contestant's behaviour during an interaction. Aggressive competitor behaviour could escalate a competitive interaction, or it could elicit a nonaggressive escape response from the other contestant (reviewed in Schelling 1960).

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To determine how competitor behaviour affects the context of an interaction, experiments must decouple a competitor's presence and its behaviour during interactions in various contexts. Separating a competitor's presence and behaviour, however, is difficult. For example, in both noninteractive (fixed stimulus presentation) and interactive (stimulus presentation modified according to subject behaviour) playback experiments, the playbacks themselves can convey more information to the test subject than mere presence. The stimuli of playbacks can indicate a competitor's intended behaviour (aggressive or otherwise), which could then affect the test subject's behaviour (e.g. de Kort & ten Cate 2001; Wilson et al. 2001; Winfelder 2001; Ord & Evans 2002). Furthermore, experiments that incorporate both encounter interactions and playback stimuli show that actual encounters between competitors can provide investigators with information regarding behaviours during interactions that could have been missed by playback experiments alone (e.g. Martin & Martin 2001).

This study investigates how competitor behaviour, competitor familiarity, resource value and/or habitat type, and fighting ability all contribute to the context affecting interspecific aggressive behaviour between two closely related ant species (*Formica integroides* and *F. xerophila*) that regularly compete for access to resources (Tanner 2008a). Because aggression experiments between these two species can be manipulated to control for each factor independently, this is an ideal model system for investigating how context affects aggression between competing species.

First, we performed aggression assays in neutral arenas using live ants either from their nests or from trees that they defended as territories. This type of behavioural assay is commonly used to describe competitive interactions between ants (Langen et al. 2000; Suarez et al. 2002; Tsutsui et al. 2003; Dahbi et al. 2005) as well as many other animal species such as mammals (Getz et al. 1981; Schulte-Hostedde & Millar 2002), reptiles (Jaeger 1981; Martin & Lopez 2007) and fish (Draud & Lynch 2002; Triefenbach & Zakon 2007). Although neutral arena experiments between two live competitors have been used successfully to investigate how factors such as competitor familiarity and fighting ability can affect aggression, by themselves these assays may fail to detect key contextual components of competitive interactions such as competitor behaviour, habitat type and/or resource value (discussed by Gravel et al. 2004). Here we expand the capacity to investigate context-sensitive aggression by combining live ant assays in neutral arenas with assays using artificial competitors (glass beads coated with competitor surface lipids) both in neutral arenas and in territories of each ant species. Surface lipids provide ant recognition signals, and ants respond similarly to live ants and glass beads coated with surface chemical compounds (Lahav et al. 1999; Greene & Gordon 2007). Therefore, a live ant perceives an artificial competitor as a real competitor and responds to its presence but not to any confounding competitor behaviours. By comparing tests between live ants with tests between a live ant and an artificial competitor at various locations, we were able to isolate the unilateral action of an individual towards its competitor under a variety of contexts.

After controlling for the effects of competitor behaviour, aggression towards competitors for both species should be higher for more valuable resources or habitat types (Reeve 1989; Rodriguez 1995). The effect of competitor familiarity on aggressive behaviour, however, is less predictable. Evidence suggests that, across taxa, familiarity can either increase (Müller & Manser 2007; Thomas et al. 2007) or decrease (Fisher 1954; Jaeger 1981; Gordon 1989; Langen et al. 2000) aggression between competitors (examples of both cases reviewed in Ydenberg et al. 1988; Temeles 1994). We are not aware of any study that has investigated the combined effects of competitor behaviour, competitor familiarity and resource value on interspecific aggression.

METHODS

The field site was located in Utah, U.S.A. (41°03.650'N, 111°34.450'W, 1600 m). Cottonwood trees (*Populus angustifolia*, *P. fremontii* and hybrids of these two species) are distributed in rows and columns uniformly spaced approximately 3 m apart (described in Keim et al. 1989). Clusters of *P. angustifolia* and backcross hybrid trees, which are superior for aphid tending by both ant species (Wimp & Whitham 2001), are separated by large expanses (≥ 20 m between clusters) of trees not suitable for aphids. Both ant species' nests are located in the soil within 8 m of clusters of trees with aphids. Each cluster contains either one colony (of *F. xerophila*) or two colonies (one *F. xerophila* and one *F. integroides*) with overlapping home ranges (Powell 2000; Tanner 2008a), and ants do not travel outside of a tree cluster to forage on trees with aphids. Where their home ranges overlap, both colonies defend multiple trees as absolute territories intermingled in a mosaic pattern (Room 1971; Majer 1976; Tanner 2008a, in press). Therefore, interspecific encounters within the same cluster of trees are likely, while workers from different clusters rarely, if ever, encounter each other. For this study, we used ants from tree clusters containing both species (neighbours), and clusters 20–40 m distant with only an *F. xerophila* colony (strangers). We performed these experiments in two different years (summer 2007 and spring 2008). The first year, we compared ants' behaviours between one *F. integroides* colony with one *F. xerophila* neighbour colony and one *F. xerophila* stranger colony. The second year we expanded the study to include the original *F. integroides* and *F. xerophila* neighbour/stranger colonies and two additional *F. integroides* and *F. xerophila* neighbour/stranger colony pairs. All behaviour assays focus on heterospecific interactions (preliminary studies suggest that neither species shows conspecific aggression between colonies).

At this site, *F. xerophila* foragers were monomorphic in body size (~6 mm long), while *F. integroides* foragers were polymorphic, with a bimodal size distribution (peaks at 6 and 9 mm) (Tanner 2008a). Large *F. integroides* are involved in resource defence; therefore, all *F. integroides* used in this study were large (≥ 8 mm).

Live Ant–Ant Behaviour Assays

To determine whether arboreal ants (those defending trees) discriminate between competitors based on familiarity, we performed neutral arena behaviour assays using pairs of live interspecific competitors. We took ants from trees where they were tending aphids and simultaneously placed them in a round arena (5 cm diameter). A thin layer of soil on the arena bottom was changed between each trial. We scored behaviours of each ant for the first encounter in the following manner: (1) retreat: move quickly in the opposite direction to avoid contact; (2) ignore: no response to competitor; (3) inspect: prolonged antennae contact; and (4) fight: aggressive behaviour such as biting. A retreat by one ant was scored as 'ignore' for its competitor if the competitor showed no obvious change in behaviour. We recorded behaviours of only the first encounter (<120 s for each trial) to remove the potential for habituation between competitors (Langen et al. 2000; Grangier et al. 2007). In 2007, we performed 40 assays between neighbour *F. integroides* and *F. xerophila* pairs and 40 assays between stranger *F. integroides* and *F. xerophila* pairs. In 2008, we performed 30 assays (10 per colony pairing) between neighbour *F. integroides* and *F. xerophila* and 30 assays (10 per colony pairing) between stranger *F. integroides* and *F. xerophila*. To determine whether competitor familiarity affects ant behaviour, in 2007 we compared behaviours towards neighbours and strangers using Fisher's exact tests followed by a sequential Bonferroni correction (Rice 1989), and in 2008 we used Cochran–Mantel–Haenszel tests to test the association between competitor familiarity and

behaviour across nest pairs (Agresti 2002; R Development Core Team 2007).

To determine whether nest ants (those that emerge from the nest when disturbed) discriminate between competitors based on familiarity, in both years, we repeated the above procedures and analyses using nest ants versus arboreal competitors. Individual ants were taken from their nest entrance (~2 min after lightly disturbing the entrance with the tip of an aspirator) and placed in a neutral arena simultaneously with an arboreal competitor (neighbour or stranger).

Ant–Bead Behaviour Assays

To investigate individual behaviour in the absence of potentially confounding competitor behaviour, we made 'artificial ant competitors' by coating glass beads with ant surface lipid extracts following a modified protocol of Greene & Gordon (2003). We rinsed arboreal ants in hexanes for ~8 min, replaced ant bodies with oval-shaped borosilicate glass beads (1.5 × 6 mm) in a 1:1 ratio, and allowed the hexane to evaporate while gently shaking the vial. Because ant surface chemistry differs between species as well as between conspecific colonies (Lahav et al. 1999), we made colony-specific beads for *F. integroides*, neighbour *F. xerophila* and stranger *F. xerophila*. We used red beads for *F. integroides* and black beads for *F. xerophila* to match actual ant colours. To ensure that beads resembled the surface chemistry of their live ant counterparts, in 2007 we compared several 'artificial competitor' beads to live ants using gas chromatography–mass spectroscopy (Tanner 2008b).

We first used these beads to replicate the live-ant neutral arena assays described in the previous section. In 2007, we followed the same procedure, but replaced one ant in each assay with its glass bead counterpart. We replicated these arena assays 40 times for each of the eight pairwise combinations (arboreal *F. integroides* versus neighbour bead, arboreal *F. integroides* versus stranger bead, arboreal *F. xerophila* versus neighbour bead, arboreal *F. xerophila* versus stranger bead, nest *F. integroides* versus neighbour bead, nest *F. integroides* versus stranger bead, nest *F. xerophila* versus neighbour bead, and nest *F. xerophila* versus stranger bead). In 2008, we modified the 2007 procedure by including ants from the three nest pairs (15 assays of each pairwise combination per nest pair). Additionally in 2008, assays with artificial competitor beads were scored blind (beads were given a code for treatment group and applied in a randomized order to behaviour assays). As a control in each year, we replicated the entire ant–bead arena experiment using beads coated only with hexane solvent. In both years, ant behaviour towards control beads was significantly different from that towards treatment beads ($P < 0.003$ in all cases), and no group of ants differed from other groups in its behaviour towards control beads ($P > 0.75$ in all cases). Although a few ants (1–2) were aggressive towards control beads in almost every assay group, both *F. xerophila* and *F. integroides* (from trees and nests) frequently either inspected or ignored control beads in both the 2007 and 2008 experiments.

To determine whether habitat type and/or resource value during a competitive interaction affects ant behaviour, we then performed ant–bead assays in the field (on trees defended by ants and near their nest entrances). Each bead had a small hole perpendicular to the lengthwise axis and could be pinned to either a leaf or the ground. Prior to attaching a bead, we removed all ants from the area. We scored the behaviour of the first ant to encounter the bead (large ants only for *F. integroides*) using the same scoring scheme as described in the neutral arena assays (retreat, ignore, inspect, or fight). In 2007, we replicated this procedure 40 times for each of the four competitor bead types on trees (*F. integroides* neighbour and stranger on trees defended by *F. xerophila*; *F. xerophila* neighbour

and stranger on trees defended by *F. integroides*) as well as the four competitor bead types near nests. In 2008, we replicated this procedure 45 times for each bead type on trees and near nests (15 times per nest pair) in a randomized order with coded beads as described above. We also replicated these experiments using control hexane-rinsed beads each year.

To determine whether competitor familiarity affects ant behaviour towards 'artificial competitors', in 2007 we compared ants' behaviour towards neighbours and strangers separately for assays in arenas and on trees using Fisher's exact tests. For the 2008 data, we compared ants' behaviour towards neighbours and strangers using Cochran–Mantel–Haenszel tests. We performed the same analyses for 2007 and 2008 as described above to determine whether assay location (neutral arena or tree/nest) affects ant behaviour within a competitor familiarity category (neighbour or stranger).

RESULTS

Live Ant–Ant Behaviour Assays

In both years, differences in ant behaviours were due to greater numbers of fights between strangers than between neighbours. The behaviour of live arboreal *F. integroides* in neutral arena assays with live neighbour *F. xerophila* differed significantly from their behaviour in assays with live stranger *F. xerophila* in both 2007 (Fisher's exact test: $N = 80$, $P < 0.001$, $P_{\text{critical}} = 0.025$; Fig. 1a) and 2008 (Cochran–Mantel–Haenszel test: $M_3^2 = 21.94$, $N = 60$, $P < 0.001$; Fig. 2a), and there was no interaction between *F. integroides* nest, competitor familiarity and behaviour in 2008 (Woolf's test: $\chi_2^2 = 0.005$, $P = 0.997$) (Meyer et al. 2008). Likewise, the behaviour of live arboreal *F. xerophila* towards live neighbour *F. integroides* differed from that towards stranger *F. integroides* in both 2007 (Fisher's exact test: $N = 80$, $P < 0.001$, $P_{\text{critical}} = 0.05$; Fig. 1b) and 2008 (Cochran–Mantel–Haenszel test: $M_3^2 = 18.47$, $N = 60$, $P < 0.001$; Fig. 2b), and there was no interaction between *F. xerophila* nest, competitor familiarity and behaviour in 2008 (Woolf's test: $\chi_2^2 = 0.159$, $P = 0.924$).

Behaviour of live nest ants was not affected by familiarity of live arboreal competitors in 2007 (Fisher's exact test: nest *F. integroides* versus arboreal *F. xerophila*: $N = 80$, $P = 1$; nest *F. xerophila* versus arboreal *F. integroides*: $N = 80$, $P = 0.568$; Fig. 1c, d) or 2008 (Cochran–Mantel–Haenszel test: nest *F. integroides* versus arboreal *F. xerophila*: $M_1^2 = 0$, $N = 60$, $P = 1$; nest *F. xerophila* versus arboreal *F. integroides*: $M_2^2 = 1.924$, $N = 60$, $P = 0.3821$; Fig. 2c, d). In both years, nest ants were consistently aggressive towards both neighbour and stranger competitors.

Ant–Bead Behaviour Assays

Competitor familiarity did not affect *F. integroides* behaviour for the 2007 assays in arenas (Fisher's exact test: $N = 80$, $P = 0.833$) or trees ($N = 80$, $P = 0.806$) (Fig. 3a), nor did familiarity affect *F. integroides* behaviour for the 2008 assays in arenas (Cochran–Mantel–Haenszel test: $M_2^2 = 0.053$, $N = 90$, $P = 0.974$) or trees ($M_2^2 = 0.248$, $N = 90$, $P = 0.883$) (Fig. 4a). There was no interaction between *F. integroides* nest site, competitor familiarity and behaviour for 2008 assays in arenas (Woolf's test: $\chi_2^2 = 0.361$, $P = 0.835$) or trees ($\chi_2^2 = 0.885$, $P = 0.643$).

Competitor familiarity did, however, affect *F. xerophila* behaviour for the 2007 assays in arenas (Fisher's exact test: $N = 80$, $P < 0.001$) and trees ($N = 80$, $P < 0.001$) (Fig. 3b), as well as the 2008 assays in arenas (Cochran–Mantel–Haenszel test: $M_2^2 = 34.79$, $N = 90$, $P < 0.001$) and trees ($M_2^2 = 17.06$, $N = 90$, $P = 0.001$) (Fig. 4b). There was no interaction between *F. xerophila* nest site, competitor familiarity, and behaviour for 2008 assays in arenas

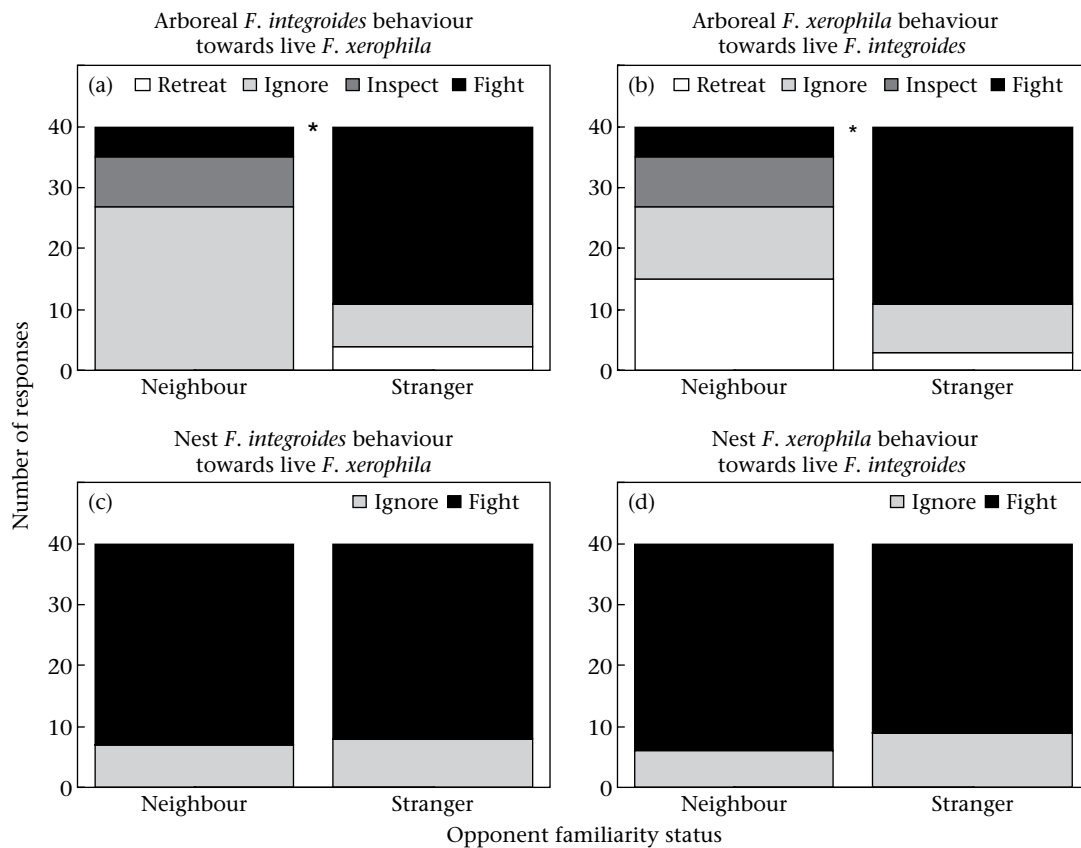


Figure 1. Behaviour counts during first encounter with live neighbour and stranger competitors for arboreal ants (a, b) and nest ants (c, d) in 2007 neutral arena assays. An asterisk denotes a significant ($P < 0.001$) difference between behaviour towards neighbour and stranger competitors (Fisher's exact test including 1 *F. integroides*, 1 *F. xerophila* neighbour and 1 *F. xerophila* stranger nest).

(Woolf's test: $\chi^2_2 = 1.513, P = 0.469$) or trees ($\chi^2_2 = 0.072, P = 0.965$). In both years, for all *F. xerophila* nests tested, and in both arena and tree assays, *F. xerophila* retreated more frequently from familiar *F. integroides* competitor beads than from unfamiliar competitor beads, and they attacked unfamiliar competitor beads more frequently than they attacked familiar competitor beads.

For *F. integroides* from the nest, competitor familiarity did not affect ant behaviour for the 2007 arena (Fisher's exact test: $N = 80, P = 0.697$) or nest ($N = 80, P = 0.873$) assays (Fig. 3c), nor did competitor familiarity affect nest *F. integroides* behaviour for the 2008 arena (Cochran–Mantel–Haenszel test: $M^2_2 = 0.245, N = 90, P = 0.885$) or nest ($M^2_2 = 1.139, N = 90, P = 0.566$) assays (Fig. 4c). There was no interaction between *F. integroides* nest site, competitor familiarity and behaviour for either the 2008 arena (Woolf's test: $\chi^2_2 = 0.418, P = 0.811$) or nest ($\chi^2_2 = 0.392, P = 0.822$) assays. *Formica integroides* from the nest frequently attacked both neighbour and stranger *F. xerophila* competitor beads.

Competitor familiarity also did not affect behaviour of *F. xerophila* from the nest in the 2007 arena (Fisher's exact test: $N = 80, P = 0.501$) or nest ($N = 80, P = 0.432$) assays (Fig. 3d), nor did competitor familiarity affect nest *F. xerophila* behavior for the 2008 arena (Cochran–Mantel–Haenszel test: $M^2_2 = 4.345, N = 90, P = 0.114$) or nest ($M^2_2 = 0, N = 90, P = 1$) assays (Fig. 4d). There was no interaction between *F. xerophila* nest site, competitor familiarity and behaviour for either the 2008 arena (Woolf's test: $\chi^2_2 = 0.476, P = 0.788$) or nest ($\chi^2_2 = 0.110, P = 0.947$) assays. As did *F. integroides*, *F. xerophila* from the nest frequently attacked both neighbour and stranger competitor beads.

For arboreal *F. xerophila*, assay location (neutral arena versus tree) sometimes affected behaviour towards neighbour and

stranger (Fisher's exact test: 2007: $P < 0.001, P = 0.0498$, respectively; Cochran–Mantel–Haenszel test: 2008: $P < 0.001, P = 0.056$, respectively) *F. integroides* beads (Figs 3b, 4b). Although more aggressive towards neighbour competitors on trees than in arenas, the weakly significant to nonsignificant effect of assay location on *F. xerophila* behaviour towards strangers in 2007 and 2008 was due primarily to the predominance of aggressive behaviour towards strangers regardless of assay location. Assay location had a mixed effect on arboreal *F. integroides* behaviour towards neighbour and stranger (Fisher's exact test: 2007: $P = 0.273, P = 0.338$, respectively; Cochran–Mantel–Haenszel test: 2008: $P = 0.003, P = 0.004$, respectively) *F. xerophila* beads (Figs 3a, 4a). The significant effect of assay location in 2008 was due primarily to ignore behaviours in arenas being replaced by inspect behaviours for ants on trees; the proportion of aggressive behaviours in these tests, however, remained similar.

For nest *F. xerophila*, assay location (neutral arena versus nest) rarely affected behaviour towards neighbour or stranger (Fisher's exact test: 2007: $P = 0.1275, P = 0.80$, respectively; Cochran–Mantel–Haenszel test: 2008: $P = 0.030, P = 0.957$, respectively) *F. integroides* beads (Figs 3d, 4d). Nest *F. xerophila* were equally aggressive towards neighbour and stranger *F. integroides* regardless of assay location, but nest *F. xerophila* in 2008 replaced ignore behaviours towards neighbour *F. integroides* in arenas with inspect behaviours near their nest. Assay location also had a mixed effect on nest *F. integroides* behaviour towards neighbour and stranger *F. xerophila* beads (Fisher's exact test: 2007: $P = 0.885, P = 0.377$, respectively; Cochran–Mantel–Haenszel test: 2008: $P = 0.002, P = 0.017$, respectively) (Figs 3c, 4c). Towards both neighbour and stranger *F. xerophila* beads, *F. integroides* replaced ignore behaviours

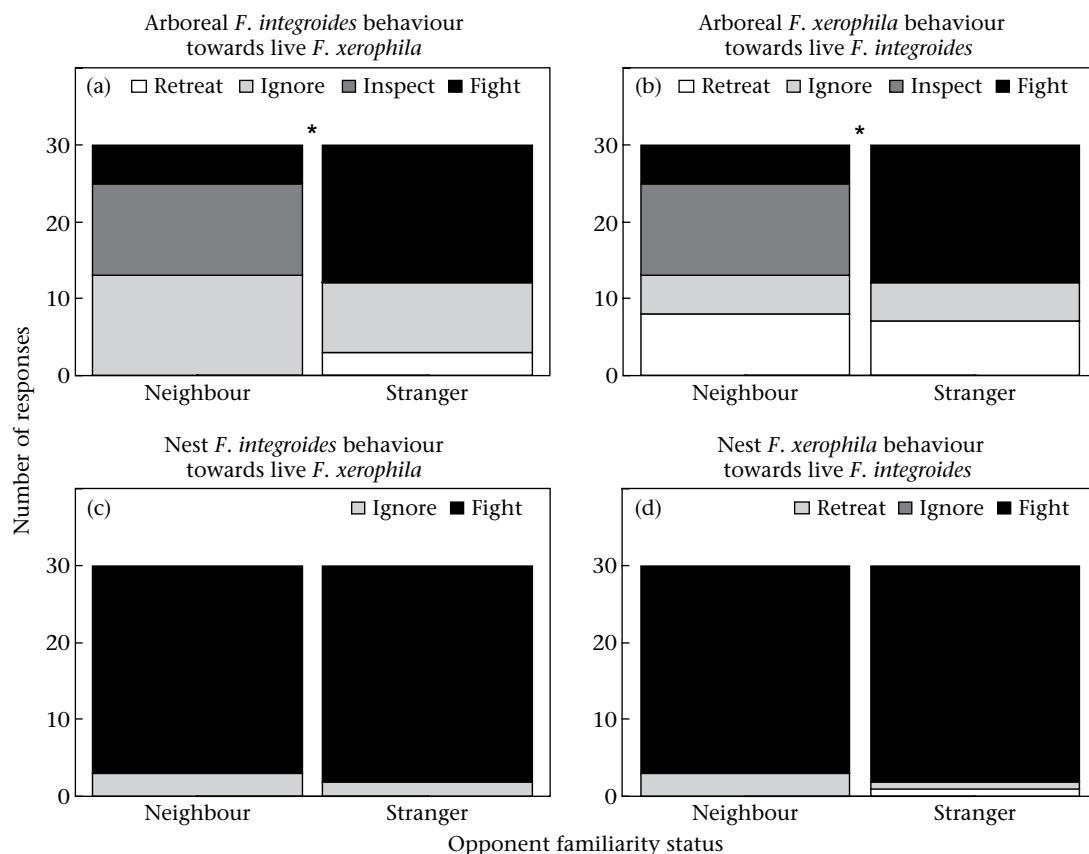


Figure 2. Behaviour counts during first encounter with live neighbour and stranger competitors for arboreal ants (a, b) and nest ants (c, d) in 2008 neutral arena assays. An asterisk denotes a significant ($P < 0.001$) difference between behaviour towards neighbour and stranger competitors (Cochran–Mantel–Haenszel test including 3 *F. integroides*, 3 *F. xerophila* neighbour and 3 *F. xerophila* stranger nests).

in arena assays with aggressive behaviours in assays near their nests. It is likely that for both the arboreal and nest ant assays, the replacement of ignore behaviours with inspect and/or fight behaviours reflects a behavioural artefact or 'arena effect' (Downes 1969) in which some ants in neutral arenas are more concerned with escape than with competitor interactions.

DISCUSSION

Results from this study suggest that a suite of factors collectively regulate aggressive behaviour in different ways for these two closely related interspecific competitors. In addition, the combination of live ant–ant and ant–bead assays provides information that neither set of experiments could provide alone.

Formica xerophila aggressive behaviour is highly context sensitive. Previous work has shown that in the same way as lions (Heinsohn 1997) and chimpanzees (Wilson et al. 2001), *F. xerophila* assess their numerical state prior to a competitive encounter, and are more aggressive when in groups than when alone (Tanner 2006, 2008b). Here we show that *F. xerophila* respond to at least three aspects of context in addition to numerical status: competitor familiarity, habitat type and resource value. Arboreal *F. xerophila* discriminate between stranger and neighbour *F. integroides*, initiating more fights with strangers and more retreats from neighbours (Figs 3b, 4b). The increased aggression towards stranger *F. integroides* may indicate an assessment that strangers represent a greater threat than neighbours to arboreal *F. xerophila* (Temeles 1994). Alternatively, *F. xerophila* and *F. integroides* neighbours could have an established dominance hierarchy, while strangers between the two species act more aggressively because of hierarchy status

mistakes (Ydenberg et al. 1988). Such reduced aggression between coexisting competitors within an established hierarchy (through repeated heterospecific contact) has been suggested to operate in various taxa such as rodents (Perri & Randall 1999) and ants (Delsinne et al. 2007).

Arboreal *F. xerophila* behaviour towards competitors is also sensitive to assay location. Arboreal *F. xerophila* were aggressive more often and retreated less during assays on their tree territories than during assays in neutral arenas (Figs 3b, 4b). This difference in behaviour towards competitors in arenas and on defended trees suggests that, similar to other competing animals (reviewed in Hölldobler & Wilson 1990; Rodriguez 1995), the location in which a competitive interaction takes place can have a profound effect on the competitors' behaviours.

In addition to different behaviours on trees and in arenas, *F. xerophila* behaviour towards *F. integroides* differed between ants defending tree territories and ants defending nest territories. Whereas ants from trees discriminated between neighbour and stranger competitors, and were sensitive to assay location, ants from the nest were frequently aggressive towards both neighbour and stranger *F. integroides* in both neutral arena and nest site assay locations (Figs 3d, 4d). Generally, aggression should increase with resource value because the cost of choosing the wrong action (e.g. being tolerant towards a competitor when aggression is needed) varies with the value of the resource being defended (Reeve 1989). If we assume a nest is more valuable than a tree with aphids, this pattern suggests that, similar to other animals (Stamps 1977; Robinson 1985; Elwood et al. 1998; Riechert 1998; Buczkowski & Silverman 2005), *F. xerophila* aggression towards competitors increases with resource value.

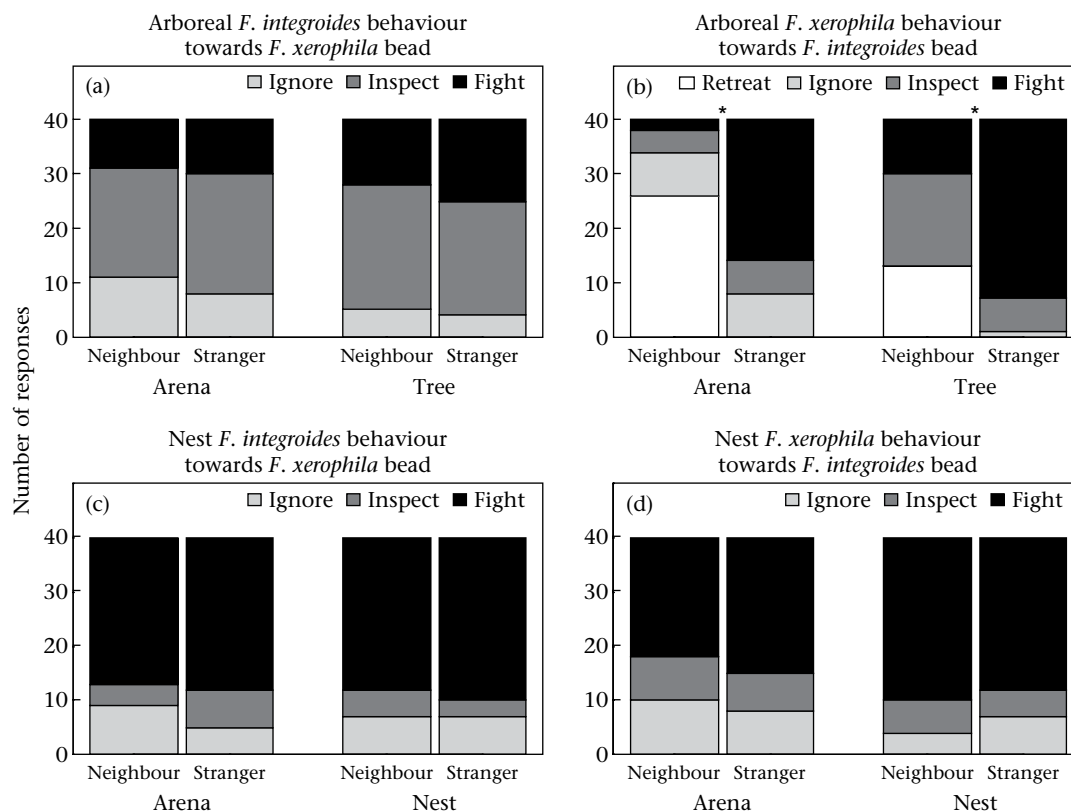


Figure 3. Behaviour counts during first encounter with 'artificial' neighbour and stranger competitor beads for arboreal ants (a, b) and nest ants (c, d) in 2007 assays on defended territories (trees or nest sites). An asterisk denotes a significant ($P < 0.001$) difference between behaviour towards neighbour and stranger competitors (Fisher's exact test including 1 *F. integroides*, 1 *F. xerophila* neighbor and 1 *F. xerophila* stranger nest).

Reduced aggression between familiar competitors could be due to repeated encounters between individuals (Delsinne et al. 2007). Additionally, a lack of nestmate communication could contribute to the difference in behaviours between arboreal and nest *F. xerophila*. Brown & Gordon (1997) suggested that neighbour recognition between ant colonies can arise either from frequent forager encounters or from nestmate communication. Although *F. xerophila* arboreal foragers distinguished neighbour from stranger *F. integroides*, this distinction was not made (or at least not acted upon) by nest *F. xerophila*. This difference between arboreal and nest ant behaviour suggests that nestmate communication (between arboreal and nest ants) does not contribute to neighbour–stranger discrimination, and frequent forager contact is a more likely explanation in this case.

Interestingly, *F. xerophila* behaviour did not appear to be affected by *F. integroides* behaviour. *Formica xerophila* behaviour towards live *F. integroides* was similar to *F. xerophila* behaviour towards artificial competitors (cf. Figs 1b, 3b arena, and Figs 2b, 4b arena). In the case of *F. xerophila*, factors such as encounter location and competitor familiarity appear to take precedence over competitor behaviour.

Like *F. xerophila*, nest-defending *F. integroides* were aggressive towards both neighbour and stranger competitors regardless of assay location, which suggests that the nest is a highly valued resource (Figs 3c, 4c). Unlike *F. xerophila*, however, arboreal *F. integroides* did not discriminate between neighbour and stranger competitors nor did they behave differently in tree and neutral arena assays (Figs 3a, 4a). When arboreal *F. integroides* encountered either neighbour or stranger *F. xerophila* beads, *F. integroides* typically responded by inspecting the perceived competitor (Figs 3a, 4a). This initial inspecting behaviour, together with the large number of live ant fights between strangers (Figs 1a, 2a), suggests

that arboreal *F. integroides* use a Tit-For-Tat (TFT) strategy in which they reciprocate the behaviour of their competitor (in this case, 'defect' = fight and 'cooperate' = do not fight). Therefore, *F. integroides* behaviour is notably affected by its competitor's behaviour. The TFT strategy has been observed in a wide range of intraspecific interactions (Dugatkin 1998), but it has not been reported for interspecific aggression as far as we know.

The combination of *F. integroides* TFT strategy and *F. xerophila* neighbour/stranger discrimination produces a potentially misleading result when live individuals are used in assays. Live ant assay results suggest that *F. integroides* show a dear enemy strategy (Fisher 1954) by acting more aggressively towards stranger *F. xerophila* than neighbours (Figs 1a, 2a). Examination of each species' behaviour while controlling for confounding competitor behaviour reveals that this dear enemy interpretation is incorrect. Our results indicate that fights in the live ant assays (Figs 1a, 2a) resulted from *F. integroides* initially inspecting its competitor, and then fighting back (reciprocating aggression with aggression) against aggressive *F. xerophila*, which are more likely to be strangers than neighbours (Figs 3b, 4b). Similarly, arboreal *F. integroides* appear to tolerate neighbour *F. xerophila* more than strangers (Figs 1a, 2a) because neighbour *F. xerophila* either inspected or retreated from *F. integroides* (Figs 3b, 4b).

How context affects competitive strategies can also be shaped by differences in the competitors' relative fighting abilities. Because initiating a fight can increase a competitor's likelihood of winning a contest (Mcauley et al. 1998; Tsutsui et al. 2003), many behaviourally dominant species are often aggressive in competitive encounters (e.g. Bleich & Price 1995; Rowles & O'Dowd 2007). A large asymmetry in fighting ability, however, may reduce the benefit of initiating aggression. If contestants' fighting abilities are skewed such that one is a much better fighter, then a fight initiated

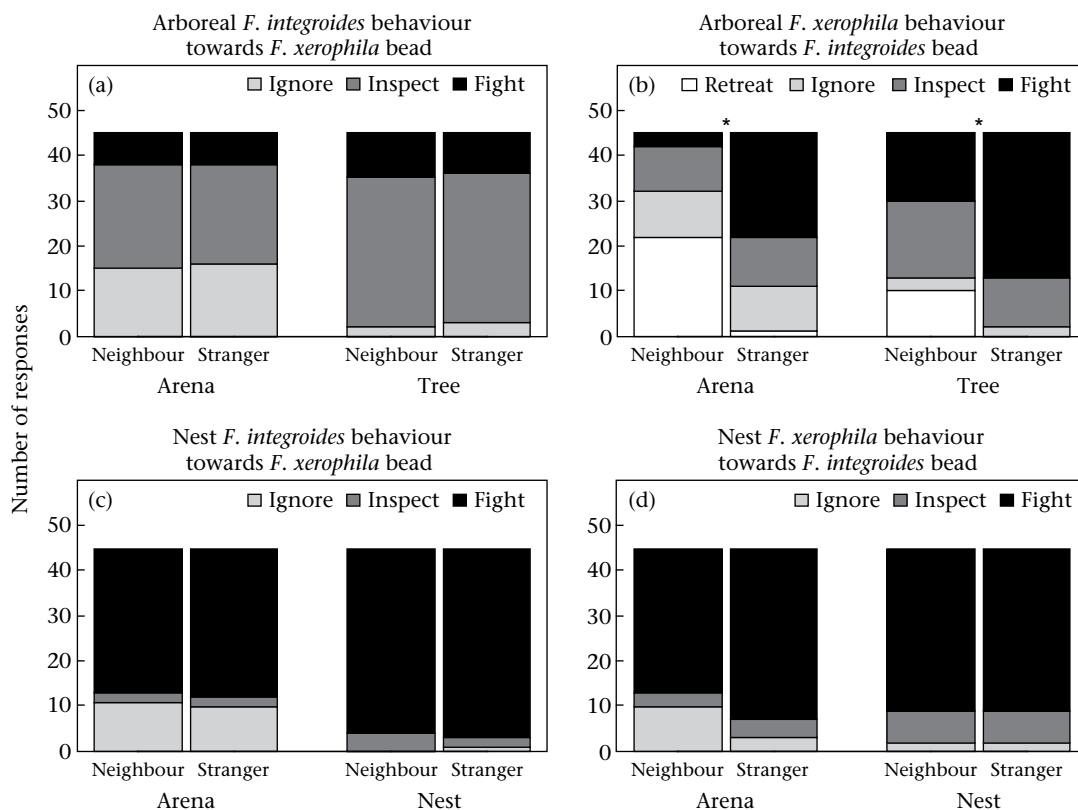


Figure 4. Behaviour counts during first encounter with 'artificial' neighbour and stranger competitor beads for arboreal ants (a, b) and nest ants (c, d) in 2008 assays on defended territories (trees or nest sites). An asterisk denotes a significant ($P < 0.001$) difference between behaviour towards neighbour and stranger competitors (Cochran–Mantel–Haenszel test including 3 *F. integroides*, 3 *F. xerophila* neighbor and 3 *F. xerophila* stranger nests).

by an inferior competitor may not pose the same risk as a fight initiated by a competitor of equal ability. Therefore, dominant contestants would not need to waste time and energy fighting every subordinate competitor, only those that acted aggressively. Consistent with this explanation, *F. integroides* regularly win dyadic interference competitive interactions with *F. xerophila* in this system (Tanner 2008a). Furthermore, *F. integroides* are part of the rufa group of the *Formica* genus, which generally is behaviourally dominant over the fusca group that includes *F. xerophila* (Savolainen et al. 1989; Savolainen 1990). This asymmetry in fighting ability could help to explain *F. integroides*' insensitivity towards contexts such as competitor familiarity and assay location.

The context-specific behaviour of *F. xerophila* may help to explain the territorial spatial structure shown by these coexisting species. Ant community structure develops largely from the degree of aggression that species show towards each other, where behaviour during competitive encounters determines whether species can coexist locally (Room 1971; Savolainen et al. 1989). Differences in aggression regarding resource defence are thought to divide communities into at least two groups: dominant territorial species that aggressively defend territory or food, and submissive species that defend only their nests (Savolainen et al. 1989; Davidson 1998). Submissive species are expected to coexist locally with dominant ones, but submissives are maintained in a community either as fugitives relegated to foraging on suboptimal resources (Sanders & Gordon 2000), at suboptimal times (Cerdá et al. 1997), or when dominant species must contend with additional threats such as parasitoids that periodically reduce their competitive abilities (LeBrun & Feener 2007). Here, *F. integroides* and *F. xerophila* share terrestrial territory by showing a dominance–discovery trade-off in which *F. xerophila* act submissively and retreat from *F. integroides* (Tanner 2008a). For arboreal resources

(trees with aphids), however, large numbers of aggressive *F. xerophila* defend entire trees as absolute spatial territories from *F. integroides*, creating a mosaic pattern of trees defended by either one species or the other, which is not characteristic behaviour for a submissive species (Tanner 2008a, in press). Furthermore, there is no evidence that trees defended by *F. xerophila* are inferior to trees defended by *F. integroides* with respect to resource quality (C. J. Tanner, unpublished data). The context-sensitive aggressive behaviour algorithm shown by *F. xerophila* helps clarify how this species utilizes different foraging and territorial strategies for different resource types. Results from this study support the position that a static dominance hierarchy for competing species (discussed in LeBrun 2005) is probably not appropriate for this community. Rather, a more dynamic, context-dependent hierarchy in which individuals involved in interspecific interactions can behave with some flexibility to habitat type, resource value and competitor behaviour provides a more accurate framework for understanding community structure.

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