



Do ship rats display predatory behaviour towards house mice?



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Control operations for invasive ship rats, *Rattus rattus*, in New Zealand forests are often followed by increased house mouse, *Mus musculus*, detections suggesting rats suppress mice. A potential mechanism is intraguild predation, either by interference competition or as simple predatory behaviour. If aggression by rats towards mice is mainly competitive, it should include threat and display features associated with, for example, intraspecific fighting. If predatory, it should lack these features and be associated with feeding. In the first of two captive experiments we observed interactions between paired, live rodents, either side of a wire-mesh screen, and found that most rats were aggressive to mice. This aggression lacked threat and display characteristics typical of encounters with conspecifics and was rarely reciprocated by mice. In a second experiment, euthanized mice were drawn by a line through cages occupied by rats fed either a restricted or unrestricted diet. Rats of both groups attacked and restrained the euthanized mice, and all rats that interacted with the mice ate at least part of them, although food-restricted rats tended to eat more. As the aggressive response of ship rats towards mice lacked threat and display features and was related to feeding, we conclude that it resembles predatory behaviour. Our findings provide a better understanding of the interactions between ship rats and house mice, which hinder their management where they coexist as damaging invaders. However, further research is required to determine whether the results of our captive experiments are consistent with wild rat behaviour.

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Intraguild (IG) predation describes a relationship between species that have overlapping resource requirements, and are thus potential competitors, but that also kill and eat one another (Polis et al. 1989). IG predation may be primarily a mechanism to reduce competition, in which case it can be considered as an extreme form of interference competition involving territorial aggression or resource defence (Polis et al. 1989; Sunde et al. 1999). Alternatively, reduced competition may be an incidental consequence of opportunistic feeding behaviour in which case aggression is predatory (Polis et al. 1989; Stapp 1997). Identifying IG predation and distinguishing between these drivers can be complex, particularly for small, elusive species, but allows a better understanding of the dynamics of interspecific relationships (Stapp 1997).

IG predation is observed most frequently among generalist predators (Polis et al. 1989). Most rodent species are granivorous or herbivorous, but some have a more varied omnivorous diet (Landry

1970; Stapp 1997), including two of the most notorious, adaptable invasive rodents, the ship rat, *Rattus rattus* (also known as black rat or roof rat) and house mouse, *Mus musculus*. Their long commensal association with humans has carried these species far beyond their natural ranges, including introduction to New Zealand (Towns et al. 2006).

Field evidence suggests that interactions with ship rats influence the abundance and distribution of house mice (Innes et al. 1995; King et al. 1996a; Harris & Macdonald 2007). Competition between them is possible because their diets overlap (Ruscoe & Murphy 2005), but there is also evidence that ship rats are aggressive towards and may even be predators of mice (Lidicker 1976; Granjon & Cheylan 1988; McQueen & Lawrence 2008). Interactions between ship rats and house mice hinder how they are monitored and controlled as pests (Innes et al. 1995; Tompkins & Veltman 2006; Caut et al. 2007; Harris & Macdonald 2007; Witmer et al. 2007; Harper & Cabrera 2010). Understanding the mechanism underpinning the interaction between them could help to improve management techniques. It is unknown whether aggression and killing of mice is common among ship rats, and whether it is primarily an extreme form of interference competition or simple predatory aggression.

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Mouse-killing behaviour ('muricide') has been studied intensively in Norway rats, *Rattus norvegicus*, and is considered predatory in nature (O'Boyle 1974), for two main reasons: (1) it lacks characteristics such as threat and display postures that typify other forms of aggression such as territorial fighting during intraspecific encounters, and (2) it is associated with feeding, as Norway rats usually at least partially consume the mice they kill, especially if they are hungry (Karli 1956; Paul 1972; O'Boyle 1974).

Ship rats (average 120–160 g, Innes 2005a) are generally smaller than Norway rats (average 200–400 g, Innes 2005b), and considered less aggressive (King et al. 2011). However, they are still considerably larger than house mice (average 15–20 g, Ruscoe & Murphy 2005). The aim of this study was to determine whether ship rats are aggressively dominant to house mice and, if so, whether such behaviour shows features similar to that of Norway rats, and hence is predatory.

It is difficult, in practice, to observe direct interactions between small, nocturnal mammals under natural conditions and ethically unacceptable to stage such interactions in captivity. To circumvent these difficulties we carried out two experiments to address our research questions indirectly. In experiment 1 we observed interactions between paired, live rodents either side of a wire-mesh screen, which allowed close but not direct contact, and compared characteristics of intraspecific and interspecific encounters. In experiment 2 we investigated any link between aggression and feeding by moving a freshly euthanized mouse through the enclosures of rats in the hope that they would perceive the mouse to be alive, thus allowing us to distinguish any predatory attack behaviour from simple scavenging. We studied the response of rats on different feeding regimes to euthanized mice and to live house mouse and conspecific opponents.

If ship rats perceived mice predominantly as a competitor, we expected that they might react aggressively towards them during experiment 1 and that rats would exhibit defensive display postures similar to those shown when encountering an unknown conspecific. If rats perceived mice as prey we expected an aggressive response that lacked threat and display postures in experiment 1 and an attack on euthanized mice in experiment 2 followed by consumption.

METHODS

Trapping and Housing of Animals

We live-trapped wild mice and ship rats for experiments at intervals in spring and summer from 2008 to 2011, at forested sites near Hamilton (Waikato region, North Island). Trapping sites for mice were separated by at least 300 m and for rats by 600 m, which exceeds home range length for these animals (Innes 2005a; Ruscoe & Murphy 2005). Hence we could set up paired trials with animals that were unlikely to be familiar with each other.

To capture mice we used Longworth live-capture traps (Penlon Ltd, Oxford, U.K.) and for rats we set wire cage traps (generic make, 200 × 200 mm and 300 mm high). Both trap types exclude predators. We placed polyester fibre in the nest chamber of Longworth traps for mice and secured a container within cage traps to provide shelter for rats. We baited all traps with carrot and peanut butter and checked them early each morning. As these species are mainly nocturnal, this meant that animals should not have been detained in traps longer than 12 h, as recommended by best practice to minimize any negative effects on pregnant or lactating females and their offspring (Gurnell & Flowerdew 2006).

We examined captured animals and released females that were obviously pregnant or lactating. Mice that were suitable for the

experiment were placed in plastic containers with air holes in the lids and polyester fibre bedding. Ship rats were transported within their cage traps, which had the doors secured and were covered with a dark cloth to minimize stress. Animals were taken to the University of Waikato animal house facility. In total 65 mice and 54 rats were captured and used in experiments (including the preliminary experiment described in Appendix 1) and associated pilot trials.

We housed mice individually in laboratory-style mouse cages (300 × 200 mm and 200 mm high) and provided them with pine shavings and shredded newspaper for bedding. We housed rats individually in wire cages (600 × 800 mm and 400 mm high) and provided them with nest tubes containing shredded newspaper. We kept mice and rats in separate rooms, and we also divided intraspecific subjects and opponents into different rooms (rats) or separate parts of the same room (mice). We kept animals on a 12:12 h switched light:dark cycle (lights on 2100 hours). They were fed rodent lab pellets, oats, crisped rice, wild birdseed, pumpkin seeds, sunflower seeds, raisins, peanuts, cat biscuits and fresh carrot. Fresh water was available at all times.

We kept animals for a 2-week habituation period after which we reweighed and examined them prior to trials. At this time females that were pregnant when trapped, but in the early stages and therefore not noted, were identified. These females were used in trials once they had given birth and following a 2-week recovery period. This ensured they were maintaining weight and appeared healthy.

Experiment 1

Procedure

In a glass terrarium (600 × 300 mm and 300 mm high) we secured a wire-mesh divider (20 × 6 mm mesh gap) across the centre to bisect it, and placed a lid on top. We ran trials in a quiet, dark room and recorded the results with a near infrared (NIR) video camera and light.

Trials consisted of two phases. Phase 1 began with one animal in either half of the terrarium, and a solid partition alongside the wire divider to prevent initial contact. We left the room for a 30 min undisturbed habituation period, and then we removed the solid partition for 30 min to permit interactions. In phase 2 of the trial we replaced the partition for a 30 min rest period before removing it again for a second 30 min encounter time. At the end of each trial we returned animals to their cages and cleaned the terrarium.

Subjects were eight rats and eight mice (all adults, with even sex ratio). We randomly paired same-sex animals from this group for interspecific trials. For intraspecific trials, we paired each subject animal with a same-sex, unfamiliar conspecific from a separate group of opponent animals. Each subject therefore took part in two trials, which were presented in a random order. A preliminary study, using the same procedure, was carried out to investigate more thoroughly sex-related, and for mice age-related, differences in behaviour during interspecific encounters (see Appendix 1).

Analyses

We used behaviour sampling (Martin & Bateson 2007) to record instances in the video footage when animals interacted, defined as any occasion on which they came so close together on either side of the wire divider that, if it had not been in place, they could have made contact. For clarity, we refer to 'interactions' as these moments of close (but not direct) contact, and 'encounters' as the entire period when animals were exposed to each other and could potentially interact.

Following Blaustein (1980) we recorded which animal initiated each interaction by approaching its opponent, and which one

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