Dissipation of kin discrimination in Orkney voles, *Microtus arvalis orcadensis*: a laboratory study

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Field experiments testing the roles of relatedness in vole demography make different assumptions on the ability of voles to recognize their unfamiliar kin and this may have contributed to their contrasting outcomes. We measured the rate of dissipation of discrimination between related male and between related female Orkney voles (*Microtus arvalis orcadensis*) after increasing periods of separation to test these assumptions. Females showed a decreasing preference for the odour of their sisters as familiarity for new cage-mates increased and an increasing preference for their new cage-mates as familiarity increased. In contrast, males showed no such changes in their avoidance of their brothers following separation. Dissipation of kin-discrimination by Orkney voles in absence of reinforcement by familiarity is therefore rapid and familiarity established in adult life seemingly has the same impact on preference between females as relatedness.

1. Introduction

The ability to recognise and discriminate kin is well established in many species (Waldmann 1988). Familiarity based on association prior to weaning is the main cue that all microtine rodents studied to date use to identify kinship (Blaustein *et al.* 1987ab, Ferkin 1990). The proximate cue for familiarity among microtine rodents may be olfactory (Ferkin 1989), and familiar nest mates are perceived as close relatives, whereas unfamiliar siblings are not (Gavish *et al.* 1984, Boyd & Blaustein 1985, Ferkin 1989, Ferkin & Rutka 1990).

The ecological consequences of recognition are controversial in microtines (Ferkin *et al.* 1992, Ostfeld 1992). Differential behaviour between kin and non-kin operating within isolated groups of voles at low density (Charnov & Finerty 1981), or between related females when female territoriality limits the number of females able to reproduce in spring (Lambin & Krebs 1991a, 1993) has been implicated as a possible contributing factor to the large-scale changes in density characteristic of many microtine populations. Seasonal changes in the degree of territoriality among female microtines are associated with changes in the degree of relatedness (Lambin & Krebs 1991b, Salvioni & Lidicker 1995). However, the use of familiarity as a cue for kin recognition imposes some limitations on the prevalence of differential behaviour between kin and non-kin in vole populations.

If familiarity acquired before weaning and reinforced by social interaction after weaning is the main cue for kin-recognition, then related individuals must not recognise their close kin if they

have not been in contact for a protracted period (Ferkin *et al.* 1992). Relatedness without familiarity is likely to occur following the dispersal of a family member, between fathers and daughters since paternal care is rare in microtines, or between siblings from different litters who have not shared the same rearing environment. The prevalence of such cryptic relatedness is likely to depend upon the rate of dissipation of the ability to recognise kin following separation (Ferkin *et al.* 1992). Dissipation of kin recognition, measured by the prevalence of incest avoidance in intersexual pairings of prairie voles (*Microtus ochrogaster*), is influenced by the length of separation and by the length of time over which associations were established (Gavish *et al.* 1984). Cryptic relatedness restricts the consequences of differential behaviour between kin and non-kin to individuals who are both philopatric and familiar (Ferkin *et al.* 1992, Ostfeld 1992). The relationship between closely related philopatric (hence familiar) females is thought to be responsible for the flexibility in social systems of microtines with possible demographic consequences (Lambin & Krebs 1991a, Wolff 1993).

It is possible that familiarity established by a post-weaning association between unrelated individuals has the same effect on the nature of interactions as do associations established pre-weaning between related individuals. Common rearing usually is assumed to be the critical time for the establishment of kin recognition (Ferkin 1990, Ferkin & Rutka 1990) but, surprisingly, this has not been the subject of any formal test with microtines. If common rearing is a prerequisite for recognition, then non-littermate full siblings will be unable to recognise each other as kin. On the other hand, if the relative impact of familiarity in adult life alone is similar to that of relatedness reinforced by familiarity, the impact of relatedness on vole social systems and demography would be smaller than currently believed. For instance, adult individuals joining over-wintering social groups such as those formed by meadow voles (*Microtus pennsylvanicus*) during the non-breeding season (Madison *et al.* 1984) would behave as if they were related and any disruption caused by an unrelated immigrant would dissipate after the immigrant had become established within the group and become familiar with its members.

The validity of field experiments exploring the consequences of differences in kinship on the demography of vole populations is critically dependent on the assumptions made about the proximate cue for kin recognition by voles, and on the rate of dissipation of kin discrimination. Experiments relying on the release of related and unrelated individuals in enclosures (Boonstra & Hogg 1988, Ylönen *et al.* 1990, Sera & Gaines 1994, Mappes *et al.* 1995, Pusenius & Viitala 1995) differ in this respect and this has not been recognised in a recent review of these experiments (Wolff 1995). Specifically, the validity of the assumptions made on (i) the ability of voles to recognise relatives that may be unfamiliar (Boonstra & Hogg 1988), (ii) the length of time necessary for unrelated familiar individuals to be treated as relatives (Ylönen *et al.* 1990), and (iii) the prevalence of kin-based behavioural asymmetries between males (Wolff 1995) could explain the contradictory outcomes of these experiments.

In this paper, we report on a laboratory experiment designed to measure the rate of dissipation of discrimination between odours of related male and between related female Orkney voles (*Microtus arvalis orcadensis*) after increasing periods of separation. Like their counterparts from mainland Europe, Orkney voles are highly social, and breeding females form clusters that may be based on matrilines (Langsdale, Young & Lambin unpub.).

2. Material and methods

2.1. Experimental subjects

We used first generation Orkney voles from a captive colony established at Aberdeen University's Culterty field station with voles caught on mainland Orkney in February 1994. Voles were housed in wire mesh cages (310 mm wide × 220 mm high × 480 mm long), which contained saw-dust, a wooden nest box and nesting material. Laboratory rat cake, potato skins, carrots and water were provided ad libitum. Temperature and daylength were not controlled and followed outdoor conditions.

On 1 September 1994, we selected 39 sexually immature subadult (42–68 days old) voles from six litters with three or more same-sex individuals. Littermates had been sharing the same cage since their birth. We housed three same-sex littermates in the same cage. One week later, we randomly chose one individual from each litter group and moved it into another cage already housing two full-siblings of the same-sex and similar weight and from another

unrelated litter. In total there were nine cages, each now containing a vole separated from its littermates and housed with new cage-mates who were littermates.

2.2. Odour preference tests

Voles separated from their littermates were subjected to two odour preference tests each week during the five weeks that followed separation. We conducted odour preference tests in a covered perspex Y-maze (each arm $220 \times 120 \times 95$ mm). The choice arms were at a $60°$ angle to the common arm. Battery-operated hand-held fans fitted at the end of the choice arms produced an air current through holes (60×50 mm) perforated at the end of each choice arm. We placed nesting material with absorbed stimulus odours at the far end of each choice arm. This was in perforated tinfoil baskets to prevent the nesting material from blowing down towards the common arm. A movable partition separated the common arm from the choice arms. After each run, we thoroughly washed the maze with soapy water and 10% alcohol, rotated the whole Y-maze by $180°$ and swapped the odour stimuli from one arm to the other. We washed our hands thoroughly each time we transported bedding to a basket. Odour preference trials and paired encounters were performed in a dark room lit by a very dim red light.

Each trial consisted of 10 runs. At the start of each run, we placed a vole into the common arm, facing away from the lowered partition and the odour sources. We then left the vole in the common arm for 5 min to acclimatise to its new surroundings. We then raised the partition, and let the vole choose between the left or right arms. Each arm contained a different odour source, the home nest odour and or a foreign nest odour. A decision was defined as when the whole body of the vole entered either choice arm in order to remove any subjectivity in scoring runs. Prior to separation (Week 0), we subjected voles to a single test between the odour of bedding from their littermates (plus self) and that of unrelated unfamiliar voles, referred to as a Kin vs. Stranger test (K vs. S). After separation (Weeks 1 to 4) voles were subjected to two types of trials each week. They were offered the choice between the odour of their now separated littermates and a complete stranger to investigate the effect of decreasing familiarity on preference for kin (K vs. S). In a different test, they were offered the choice between the odour of their now separated littermates and that of current unrelated cage-mates and self (referred to as Kin vs. New (K vs. N)) to investigate the effect of increasing familiarity on preference.

We looked for relationships between the degree of preference for kin (number of choices for kin/10 runs) and the time since separation from kin by fitting generalized additive models, assuming a binomial error distribution with a logit link function to odour preference data (Collett 1991). In all analyses, trials (10 runs) were the independent samples. Separated voles were tested repeatedly at 7-day intervals (5 times) in our experiments and this could have led to spurious patterns in the data. We checked whether this was the case by sequentially introducing the identity of each vole as binary dummy variables in the logistic models. This does not amount to a repeated measure analysis but provides a test for individual differences. Models were fitted using the SAS LOGISTIC procedure with stepwise forward selection of variables.

3. Results

When offered the choice between odour stimuli from their familiar littermate sisters and unrelated, unfamiliar females, immediately following separation, females preferentially chose their kin (predicted preference on Week 0 = 0.762, lower 95% confidence limits *(c.l.)* = 0.644, upper 95% *c.l.* = 0.850, Fig. 1a). The preference by females for their kin when offered the choice between sisters of diminishing familiarity and unrelated new cage-mates of increasing familiarity (K vs. N) declined significantly following separation. The preference for kin was better described by a logistic model including time as an independent variable than by a model assuming constancy of preference over time (difference in deviance $\chi^2 = 23.94$, $df = 1$, $p = 0.0001$). One female out of four chose the odour of her sister with a consistently lower probability than the other females (difference in deviance after adding vole identity $\chi^2 = 30.91$, $df = 2$, $p = 0.001$) but showed a similar decline in preference for kin over time (Fig. 1a). The fit of the logistic model to the data is satisfactory (residual deviance $\chi^2 = 1.28$, $df = 2$, $p = 0.52$). Predicted values and their 95% confidence limits indicate that females did not express any significant discrimination for kin after 1.4 weeks, and by 3.0 weeks they expressed a significant discrimination for the odour of their unrelated new cage-mates. At the end of the experiment, the preference of females for their unrelated new cage-mates was similar to that expressed for their sisters before separation (1-fitted probability at Week 4 = 0.73, upper 95% *c.l.* = 0.82, lower 95% *c.l.* = 0.60).

The preference of females for their kin when offered the choice between their sisters and complete strangers (K vs. S) did not change following separation (Fig. 1b). Including time as an independent variable did not significantly improve the fit of a logistic model describing the probability of choosing the odour of a female's sisters (residual deviance $\chi^2 = 4.7366$, $df = 4$, $p = 0.315$).
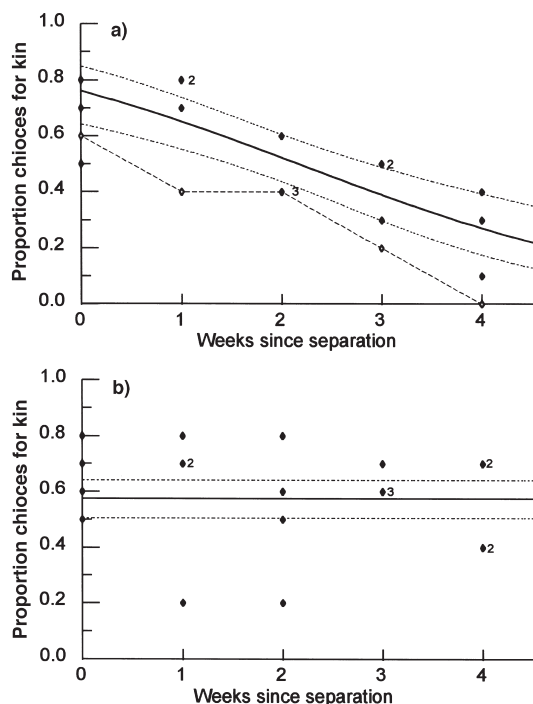
Fig. 1. Preference by females for the odour of their sisters following increasing periods of separation when: — a: tested against their unrelated new cage-mates of increasing familiarity, — b: tested against unrelated unfamiliar complete strangers. The solid line represents the probability of choosing the kin odour predicted by logistic regression and the dotted lines the 95% confidence limits. Filled symbols represent the observed proportions (out of 10 choices) and the figures by the symbols the number of individuals with the same observed proportion. The open symbols linked by a stippled line are the observations from a female with a predicted proportion (not shown) significantly lower than that of the other females. Data from Week 1 are the same in Fig. 1a and b as new cage-mates were complete strangers to the test subjects.

The predicted preference for kin (0.57, upper 95% c.l. = 0.64, lower 95% c.l. = 0.505) differs slightly but significantly from the value of 50% expected if no preference was shown.

Unlike females, males did not preferentially choose the odour of their brothers when offered the choice between stimuli from their familiar littermate brothers and unrelated unfamiliar males immediately following separation (Fig. 2a). Males avoided the odour of their kin and showed a steady significant preference for their unrelated new cage-mates throughout the 5 weeks of the experi-

ment (predicted preference for kin in K vs. N = 0.37, lower 95% c.l. = 0.30, upper 95% c.l. = 0.44, Fig. 2a). One male out of five chose the odour of his brother with a significantly different probability than other males, and showed no preference between either odour types (difference in deviance after adding vole identity $\chi^2 = 5.88$, $df = 1$, $p = 0.015$, Residual $\chi^2 = 0.56$ with df = 4, $p = 0.96$).

The degree of discrimination by males for their kin increased over time when they were offered the choice between their brothers of decreasing familiarity and complete strangers (K vs. S) (Fig. 2b). Including time as a dependent variable significantly improved the fit of a logistic model describing the probability of choosing the odour of a male's brother (difference in deviance $\chi^2 = 8.802$, $df = 1$, $p = 0.003$, Residual deviance of model with time $\chi^2 = 3.17$ $df = 1$, $p = 0.074$). Predictions of the model indicate that no more significant discrimination for unfamiliar unrelated males takes place after 0.6 weeks and that, after 3.1 weeks, males significantly discriminate in favour of the odour of their unfamiliar brothers relative to that of unfamiliar unrelated complete strangers.

4. Discussion

The present study, although based on a small sample size, reveals a clear sexual asymmetry in the degree of kin discrimination displayed by Orkney vole males and females. Females discriminate for the odour of females with whom they are familiar whereas males significantly discriminate against the odour of their brothers and of familiar males. The pattern of dissipation of discrimination towards kin following separation is also different for the sexes and the type of preference test considered reflects the above rule of preference. Females showed a decreasing preference for the odour of their sisters as familiarity for new cage-mates increased and an increasing preference for their new cage-mates as familiarity increased. In contrast, males showed no such changes in their avoidance of their brothers following separation. When choosing between the odour of their sisters and unfamiliar complete strangers, females seemingly preferred the odour of their sisters through the 4 weeks following separation. In contrast, the avoidance of the odour of their brother by males

disappeared rapidly when offered the choice between brothers of decreasing familiarity and complete strangers. Despite some differences between subjects in the degree of discrimination and a small sample size, this study reveals a high degree of consistency in the pattern of temporal change in the degree of discrimination. This pattern was well described by logistic models and any artefact caused by the repeated testing of the same individuals over 5 weeks corrected for by the inclusion of individuals in such models. Model predictions and associated confidence limits can therefore be used to predict the timing of disappearance of discrimination. A potential weakness in our experiments on the discrimination between kin or new cage-mates is the fact that we used bedding to produce odour stimuli such that the odour of self was mixed with the odour of littermates prior to separation (Week 0) and with that of new cage-mates thereafter. This could have been a confounding variable in our experiments if voles showed a preference to go down the arm of the apparatus in which one's own odour is detected. However, our results are not consistent with this possibility. The preference for kin by females followed a gradual decline over time instead of the steep step function expected if preference for self guided the choice of odour stimuli. The constancy of the preference for kin expressed by males is also not compatible with such interpretation.

Dissipation of kin-discrimination (*sensu* Waldmann 1988) by Orkney voles in the absence of reinforcement by familiarity is rapid. After being separated for only 1 week, females lost any discrimination for the odour of their sisters over the odour of their new cage-mates. Similarly, males stopped discriminating against the odour of their brothers one week after separation. However, it is does not necessarily follow from the absence of discrimination that kin-recognition has dissipated. No firm data exist on the rate of dissipation of kin recognition in other microtine species in situations where mate choice is not involved. In intersexual pairings of prairie voles (*M. ochrogaster*), a 15-day separation overcame incest avoidance for individuals that had been reared together until 50 days old (Gavish *et al.* 1984) whereas gray-tailed voles (*M. canicaudus*) that had been separated for 5 or 12 days from the partners with whom they had been reared retained their
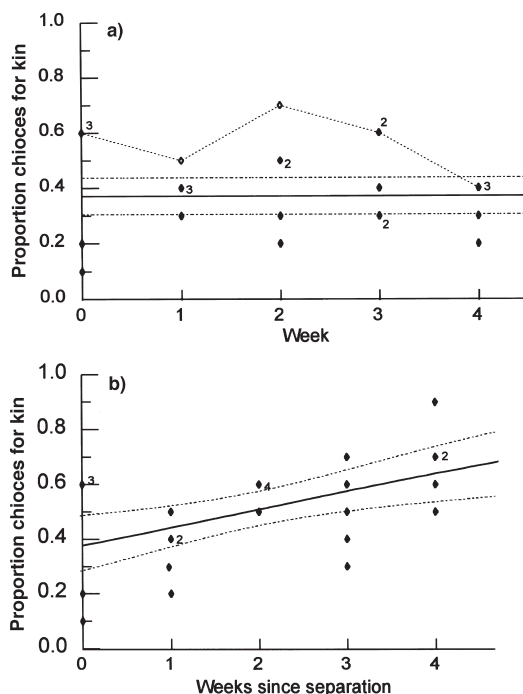

Fig. 2. Preference by males for the odour of their brothers following increasing periods of separation when: — a: tested against their unrelated new cage-mates of increasing familiarity, — b: tested against unrelated unfamiliar complete strangers. The solid line represents the probability of choosing the kin odour predicted by logistic regression and the dotted lines the 95% confidence limits. Filled symbols represent the observed proportions (out of 10 choices) and the figures by the symbols the number of individuals with the same observed proportion. The open symbols linked by a stippled line are the observations from a male with a predicted proportion (not shown) significantly lower than that of the other males. Data from Week 1 are the same in Fig. 2a and b as new cage-mates were complete strangers to the test subjects.

mating avoidance (Boyd & Blaustein 1985). However, the rapid dissipation of discrimination towards kin and the implication that most individuals loose the potential to recognise kin after dispersal are unlikely to have serious consequences in natural vole populations. Indeed, female philopatry is the rule in microtines (Boonstra *et al.* 1987) and the empirically demonstrated instances of kin discrimination in natural vole populations are restricted to individuals that are both related and familiar (Lambin 1993, 1994ab). It is most unlikely that individuals that had been separated would reunite naturally.

The observation that females preferred the odour of their new cage-mates 3 weeks after being separated from their sisters suggests that familiarity established in adult life has the same impact on preference between females as relatedness. If new cage-mates were truly perceived as kin then the period during which kin-recognition can become established must be longer than the pre-weaning period. This is supported by the observation that, in at least three *Microtus* species, captive juveniles show parental care towards their non-littermate (Solomon 1991, Powell & Fried 1992, Lambin & Stewart unpub.). Similarly, prairie voles paired when 14 days old behave as siblings and will not breed (Gavish *et al.* 1984). An alternative interpretation is that it is the closeness and not the timing of association and ensuing familiarity which triggers amicable behaviour. During the breeding season, close association such as the ones imposed by our design, might only involve members of extended matrilineal groups in natural vole populations and close association may still provide a reliable basis for kin recognition. This will not be the case for species that form winter aggregations when agonistic behaviours are reduced. At that time, any individual that moves between communal nests will become closely associated with unrelated individuals (Madison & McShea 1987, Ferkin *et al.* 1992).

After being housed together for 3 weeks, unrelated familiar female Orkney voles showed the same degree of preference for each other's odour as did related familiar females. If this is not an artefact of the close contact imposed by the experimental conditions and, if preference for odours in laboratory conditions reflects kin-based behavioural asymmetries in other microtine species, the role of relatedness in accounting for interseasonal variability in social systems (Lambin & Krebs 1991b, Wolff 1993, Salvioni & Lidicker 1995) and influencing demography (Lambin & Krebs 1991a, 1993) must be re-assessed. If familiarity is the proximate basis for relaxed aggression between females, only recent immigrants should be recipients of aggression and there should be little aggression between adjacent females that are established although unrelated (Ostfeld 1992). It is therefore possible that members of matrilineal groups gain from living in a stable social environment with familiar neighbours and little disruption by unfamiliar immigrants rather than from direct kin associations (Lambin & Krebs 1993, Agrell 1995). Further data are needed to compare the magnitude of any benefit from membership of family groups and stable social groups composed of unrelated females in natural vole populations and to ascertain to what extent aggression towards immigrants by residents reduces their ability to become established.

If members of family groups benefit mostly from living in a stable social environment, experiments relying on introducing related and unrelated voles in enclosures to study the influence of kinship on demographic traits (Boonstra & Hogg 1988, Ylönen *et al.* 1990, Sera & Gaines 1994, Mappes *et al.* 1995) do not provide a realistic approximation of the condition occurring between related and unrelated voles (Agrell 1995). Familiarity relationships may become established in both types of introductions and reduce aggression with possible demographic consequences (Ferkin *et al.* 1992). In the only experiment where a clear demographic response has been observed (Ylönen *et al.* 1990), no difference in the survival of adult or juvenile *Clethrionomys glareolus* appeared between treatments until well over 4 weeks following the release of familiar ("friends") and unfamiliar ("strangers") voles (their fig. 2). If our results with *Microtus arvalis orcadensis* apply to *Clethrionomys glareolus*, familiarity relationships could have become established in both treatments between the introduction and the appearance of differences in juvenile survival. The difference between treatments may have been a spurious consequence of the lack of treatment interspersion. Unfortunately, in a subsequent paper (Mappes *et al.* 1995), the same data have been presented in an erroneous manner together with interpolated data (their fig. 1) such that the timing of and the appearance of differences in juvenile survival between treatments is hidden.

The experiment by Ylönen *et al.* (1990) with *Clethrionomys* has been repeatedly contrasted with a similar experiment by Boonstra and Hogg (1988) with *Microtus pennsylvanicus* where no demographic response was observed (Kawata 1990, Ylönen *et al.* 1990, Ostfled 1992, Wolff 1995, Ylönen *et al.* 1995). Differences in the social system of each species or in the inclusion of familiar males by Ylönen *et al.* (1990) and not by

Boonstra and Hogg (1988) have been invoked. The present study suggests however that important differences in the assumptions used in such experiments should be considered. For instance, Boonstra and Hogg (1988) explicitly assumed that "sisters and their daughters … should recognize that they were related even though they may have been unfamiliar with each other" (p. 98). According to our results, only familiar and related females were able to discriminate/recognise each other as kin in Boonstra and Hogg's (1988) experiment. The difficulty to mimic the type of familiarity relationships that exists between related and unrelated voles in natural conditions makes it difficult to compare existing studies, relying on introducing related and unrelated voles in enclosures. Monitoring or manipulating the composition of vole populations without modifying these relationships might be a more reliable way to explore the influence of kinship on the social system and demography of microtines.

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