Kin presence drives philopatry and social aggregation in juvenile Desert Night Lizards (Xantusia vigilis)

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Kin selection is a powerful concept in evolutionary biology that can explain both cooperative and competitive behavior. Most social behavior associated with kin selection depends on prior dispersal decisions by juveniles, which can choose to either disperse away from kin or remain at the natal site. A useful way to investigate the role of kin in social behavior is to experimentally manipulate kin environment and resolve a direct causal relationship between kin presence, dispersal strategy, and subsequent social behavior. I used a cross-fostering experiment to manipulate the relatedness of the social environment in both the laboratory and the field and test for the effects of kin on juvenile dispersal and social aggregation in the Desert Night Lizard (Xantusia vigilis). I found that kin presence actively promotes both philopatry and winter aggregation, which is consistent with the predictions of kin cooperation and suggests that kin sociality in this species is not simply a by-product of limited dispersal. In combination with kin effects known in other species, these results suggest a generality of positive associations with kin, the potential dominance of cooperative over competitive mechanisms, and the increased prominence that cooperation may have in the future theoretical study of kin selection. 

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INTRODUCTION

Few concepts within evolutionary biology have generated as much attention and excitement as the theory of kin selection (Hamilton 1964). One reason for kin selection’s prominence is its power to explain both cooperative (Axelrod and Hamilton 1981) and competitive behavior (Hamilton and May 1977). Broadly defined as a form of natural selection in which an individual’s fitness is influenced by the presence or actions of genetic relatives, kin selection encompasses 2 processes: 1) kin competition, in which relatives directly compete for local resources and individuals gain fitness at the expense of their kin and 2) kin cooperation, in which association with genetic relatives increases either direct or inclusive fitness. Although the classification of a behavior as either competitive or cooperative may not be straightforward (West et al. 2007) and both types of behavior may occur simultaneously (Griffin et al. 2004; Queller 2004), identifying these processes within a system can provide insight into both the origin and maintenance of socially dependent behaviors.

The kin structure of the landscape in which both competitive and cooperative behavior occurs often depends on an individual’s choice to disperse from the natal site or remain philopatric (Hamilton 1964). Generally, a philopatric strategy results in local accumulation of close kin, whereas dispersal yields less local genetic structure and more interaction among unrelated individuals (except in examples of sibling dispersal coalitions, Sharp et al. 2008; Schoof et al. 2009; Lee et al. 2010). In fact, most well-known cooperative kin behaviors depend specifically on philopatric individuals to function from nonbreeding castes in eusocial insects (Queller and Strassmann 1998) to cooperative breeding in birds (Cockburn 1998) and alarm calling in ground squirrels (Sherman 1977; Hoogland 1996). This intimate association between dispersal strategy and kin environment yields straightforward predictions about dispersal: Kin competition should promote juvenile dispersal, whereas kin cooperation should promote natal philopatry.

However, support for competitive versus cooperative processes as a dominant driver in dispersal and social evolution varies between theoretical and empirical studies. Because dispersal was historically modeled as adaptive due to reduced competition between like individuals (Hamilton and May 1977; Frank 1986; Taylor 1988), theorists have regularly relied on kin competition to both explain dispersal and model its demographic and genetic consequences (e.g., Kîstî 2004; Bach et al. 2006). However, direct empirical evidence for kin competition driving dispersal is mixed at best (see Johnson and Gaines 1990; Lambin et al. 2001 for reviews), with many studies suggesting that kin presence promotes philopatry, particularly in vertebrates (Lambin et al. 2001; but see evidence for both in gray jays, Strickland 1991; Waite and Strickland 1997). Moreover, some of the empirical evidence in support of kin competition is correlational and does not experimentally manipulate kin environment (but see Moore et al. 2006; Cote et al. 2007). For example, several correlational studies in rodents assume that larger litter size corresponds to greater kin pressure and conclude that higher dispersal from large litters is evidence of kin competition (e.g., Ribble 1992; Jacquot and Vessey 1995). However, only a manipulation of the relatedness of litters can separate these “kin effects” on dispersal from
maternal and/or density effects through simple resource competition. While correlational studies can make important contributions, experimental manipulations are required to distinguish among potential mechanisms.

Even when interesting social behaviors among kin are empirically identified, it is often unclear whether this interaction is a cause or consequence of limited dispersal. There is a rich literature of arguments for and examples of limited dispersal correlating with both cooperative (West et al. 2001, 2006; Griffin et al. 2004) and harmful behaviors (Gardner and West 2004; Giron et al. 2004), but researchers generally do not distinguish whether individuals are interacting with kin simply because they do not disperse or if individuals do not disperse in order to increase interaction with kin (but see Eikenaar et al. 2007). This distinction is important because the former would suggest a general, perhaps indiscriminate system of social interaction, whereas the latter would necessitate a more complex social system, likely including advanced mechanisms like kin recognition.

The solution to these problems is to conduct a cross-fostering experiment in which offspring are swapped between mothers in a straightforward manipulation of kin environment. Cross-fostering has historically been used as a control for maternal effects (e.g., Brown CR and Brown MB 2000), but this manipulation can also be used to experimentally create groups with differing amounts of kin. To do this, foster individuals are released with unrelated mothers and juveniles, whereas control individuals are released with biological mothers and siblings. Following both groups of juveniles through time can then determine not only if kin presence promotes dispersal (evidence for kin competition) or philopatry (evidence for kin cooperation) but also how these dispersal strategies and kin environments affect subsequent social interactions.

I used a cross-fostering manipulation in the Desert Night Lizard (Xantusia vigilis; Figure 1a) to test for kin effects on dispersal and subsequent social behavior. Xantusia vigilis is a very small (adult mass = 1.5 g) lizard that lives at high densities in the Mojave Desert of southern California under rocks or plant cover (Stebbins 2003). I chose this species to test predictions of kin selection for 3 reasons. First, life-history characteristics of long life span (8–10 years), high survival, and a viviparous mode of reproduction not only ensure kin interactions between juveniles and mothers but also suggest long-lasting effects of iterated interactions with neighboring lizards (Miller 1951; Zweifel and Lowe 1966; Davis et al. 2011). Second, X. vigilis in the Mojave Desert likely experience high levels of competition for suitable microhabitat in the form of patchily distributed fallen Joshua tree logs (Yucca brevifolia; Figure 1b). These lizards are quite sensitive to temperatures that are common in their desert habitat (range of thermal tolerance = 0–38 °C, Gowles and Bogert 1944; incapacitated when held longer than a few minutes in hand) and cannot survive away from adequate thermal cover. Third, this species has the potential for cooperation through winter aggregation underneath logs in groups that can number 20 individuals (Zweifel and Lowe 1966; Figure 1a). Groups can contain kin or unrelated individuals, ensuring that juveniles can and do come into close contact with both relatives and nonkin, although juveniles are often found in aggregations with a parent and/or sibling (Davis et al. 2011). Previous work found that kin groups often form through the delayed dispersal of juveniles (Davis et al. 2011), but whether groups form as a by-product of generally low dispersal or whether kin actively promote delayed dispersal and subsequent social group formation was unknown.

**MATERIALS AND METHODS**

**Field collection of pregnant females**

In order to cross-foster their offspring, I collected pregnant female lizards each August in 2004–2005 (1–3 weeks before parturition; N = 128 females) from a 36 hectare plot in the western Mojave Desert near Llano, CA. An important feature of this plot is the California Aqueduct, which bisects the site from east to west. Due to its large size (12 m wide, 9 m deep), continuous flow, and long presence at the site (since the 1960s), this aqueduct has served as and still remains an effective barrier to X. vigilis dispersal between the north and south areas (corroborated by differences in microsatellite allele frequencies, Davis et al. 2011).

I hand-captured all lizards by turning fallen Joshua tree logs and finding the lizards between the log and ground or within the leaves/bark that had been resting on the ground. On capture, I placed each lizard into a 30 ml plastic temporary container marked with the latitude/longitude coordinates of the capture location using Magellan eXplorist 300 and SporTrak handheld GPS units. Because fallen logs occur at fairly high density, I then marked the individual log of capture with flagging tape that included the identification number of the lizard so that each female could be returned to her precise capture location after parturition.

On the day of capture, I measured the prenatal mass and snout-vent length (SVL) of each lizard. I also confirmed the sex of each lizard by shining a light through the base of the tail to visualize hemipenes in males (Davis and Levitt 2007). I then toe-clipped each newly captured female with a unique combination for future identification.

**Husbandry and cross-fostering**

I transported all pregnant females to the University of California, Santa Cruz (UCSC) to hold until parturition. I housed each pregnant female (average SVL = 45 mm, prenatal mass = 1.99 g) individually in 350 ml clear polypropylene containers (Fabric-Kal) with small holes drilled through the lid and sides to provide adequate ventilation. I provided a 1 cm layer of 50–50 sand/potting soil mix as substrate (changed weekly), a small piece of bark for cover, and appropriately sized crickets and waxworms

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**Figure 1**

(a) An in situ winter aggregation of 1 adult female and 1 juvenile night lizard (Xantusia vigilis) photographed immediately after lifting the sheltering log without disturbing the lizards. (b) Typical fallen Joshua tree (Yucca brevifolia) logs that serve as sites of lizard aggregation.
every 3 days. I sprayed the interior container walls with water after every feeding to provide drinking water. To facilitate lizard thermoregulation, I created a temperature gradient within each container by placing one edge of each container against a heat source (FlexWatt heat tape set at 26 °C), which cycled on a 10–14 h on-off cycle. The other edge of the container remained at room temperature of 21 °C, creating a 5 °C temperature gradient inside the container during the 10-h day. This specific temperature regime was imperative to facilitating proper fetal development and timely birth of offspring. I checked each container daily for the appearance of newborns. Within 24 h of birth, I uniquely toe-clipped and transferred each newborn (average SVL = 23 mm, mass = 0.28 g) to an individual 59 ml translucent plastic container (Dixie) at room temperature (21 °C) with otherwise identical conditions and feeding schedule as the adult females. I also measured mass, SVL, and determined the sex of each neonate immediately on collection from the female’s container.

I randomly assigned every litter of exactly 2 offspring (N = 80 litters) to either a control or foster treatment, using only females that were not used in a previous year (the remaining 47 litters contained only 1 offspring and 1 female only threw an unfertilized egg). In the foster treatment, I randomly chose and reciprocally swapped 1 of the 2 neonates from each litter between females from opposite sides of the aqueduct to ensure that the foster females were not close kin without a priori knowledge of the genetic structure of the population. Although this design does not provide complete separation of dam and sibling effects, conducting crosses of just 1 juvenile from each litter allowed me to control for both the genetic effect of the biological mother (dam) and the experimental effect of the female in each juvenile’s test group (test dam; see Statistical analysis and Supplementary Material, Supplementary Table 1).

From the perspective of each juvenile, this manipulation produced 3 kin treatments: “control” juveniles released with genetic mothers and siblings (M/S), “experimental” juveniles released with foster mothers and foster siblings (M/FS), and “by-product” juveniles with genetic mothers and foster siblings (M/FS) that necessarily resulted from the manipulation. By assigning 26 control litters and 54 experimental litters, I had 54 juveniles in the M/FS and M/FS treatments and 52 juveniles in the M/S treatment (N = 160 juveniles total). However, this experimental design specifically allowed kin environment to be coded in 3 separate ways: 1) by kin treatment described above, 2) by presence of biological mother, and 3) by presence of biological sibling in order to maximize sample size while still assessing which kind of kin environment drove differences in dispersal and social behavior (see Statistical analysis and Supplementary Material, Supplementary Table 2).

Although these treatment groups were assigned soon after birth, every lizard was housed individually from within 24 h of birth until testing (1–14 days, average = 8 days) at which point they were pooled into their assigned groups containing 1 female and 2 juveniles for laboratory experiments below and subsequent release.

Laboratory measurements of movement

Before release into the field, I measured the propensity of neonates to leave their genetic or foster mothers and travel down a track in the laboratory (Figure 2). I measured this movement distance of each neonate once after an overnight run of 12 h (7 PM–7 AM) using a binning approach that counted the number of traps crossed during the night (yielding bin scores of 0–3). Additionally, I considered any lizard found outside but not in contact with the container to be a “disperser.” I tested each group of 1 female and 2 juveniles only once in an effort to release them in the field in a timely manner.

Field measurements of dispersal and social aggregation

To estimate neonate dispersal in the field, I released all neonates in their predetermined groups at the exact capture location of the genetic or foster mother, as appropriate, within 2 weeks of birth. I then conducted mark-recapture surveys twice per year through January 2008, every summer (late August–early September) and winter (late December–early January) during the course of the study. I used the same field methods described above for collection of pregnant females, except that all lizards were immediately released at exact capture location rather than temporarily taken into captivity at UCSC. I first converted the latitude/longitude coordinates of all release and subsequent capture locations to Universal Transverse Mercator coordinates using PROJ4 v4.4.9 (http://trac.osgeo.org/proj/). I then calculated the straight-line distance between the release and furthest recapture points for each neonate (only 2 neonates were recaptured more than once, and the last capture point was the furthest from the release location for both). I considered any juvenile that traveled farther than 9.2 m to be a disperser, which represents 1.65 times the diameter of an average adult home range (following Davis et al. 2011) and corresponds to a clear natural break in the distribution of dispersal distances in this study.

To assess neonate aggregation success, I documented aggregation participation and aggregation size during winter collections. I qualified any lizards found within 0.3 m of each other as “aggregated,” although most lizards were found in direct physical contact with the other members of the aggregation when a log was lifted (see Davis et al. 2011).

Statistical analysis

I tested for effects of kin environment (3 classes: treatment, presence of biological sibling, and presence of biological mother), body size (SVL), and sex on movement probability and distance in both the laboratory and the field and aggregation frequency and group size joined in the field (6 analyses.
total; Supplementary Material, Supplementary Table 1). For the 3 analyses of probability (laboratory movement, field dispersal, and field aggregation), I constructed 15 generalized linear models (GLMs) or mixed models (GLMMs) containing the 5 main effects above and 10 appropriate interaction effects (Supplementary Material, Supplementary Table 2), linking binomial distributions. All probability models for laboratory analysis contained the same 4 random effects: biological dam, test dam, year, and days between birth and lab testing. Two of these random factors, year and days, explained none of the variance and were subsequently dropped to avoid overparameterizing the models. Year was the only random effect initially included in the field analyses of dispersal and aggregation probability, as only one set of recaptured juveniles shared either a dam or test dam. Again, this factor explained none of the variance and was dropped from the models, reducing them from GLMMs to GLMs. I then compared the Akaike information criterion (AIC) scores of these models to select the best-fit model for each analysis (excluding numerically unstable models with fitted probabilities of 0 or 1; Supplementary Material, Supplementary Table 3).

Due to the nonnormal nature of the distributions of dispersal distances and group sizes, I used 3 different approaches for the remaining 3 analyses (laboratory movement distance, field movement distance, and field group size joined). For the binned lab movement distances, I tested same 15 fixed effects in a GLMM framework with the same 4 (reduced to 2) random effects as the laboratory movement probability analysis, linked instead to a Poisson distribution and again selected the best model using AIC score. For field dispersal distances, I used a likelihood ratio test of fitted geometric distributions to test whether juveniles with and without biological siblings represented 1 or 2 statistical distributions, as no standard transformation yielded a distribution of dispersal data suitable for GLM/GLMM analysis. I conservatively preformed this analysis both with and without the one long-distance disperser (LDD) and specifically used the presence of biological siblings after finding this effect significant in the previous analysis of dispersal frequency. For group sizes joined during winter aggregation, I used a Wilcoxon signed-rank test to compare aggregation of juveniles with and without mothers and with and without siblings.

Normality of residuals was assessed using Shapiro–Wilk tests, linearity by visual assessment of residual by predicted plots, autocorrelation with Durbin–Watson tests, and homogeneity of variance with Levene’s test for all relevant analyses. Nonparametric tests were chosen where described above for data that violated assumptions of parametric analyses. Unless otherwise noted, only significant effects are reported. I performed all statistical tests in R v2.11.1 and assessed significance at $P < 0.05$.

RESULTS

Laboratory movement

I found that both movement probability and distance were influenced by an interaction between neonate SVL and presence of the biological mother (Figure 3; dispersal probability: $z = -2.025$, degrees of freedom [df] = 156, $P = 0.043$; dispersal distance: $z = -2.096$, df = 156, $P = 0.036$). Juveniles placed with foster mothers showed a steeper positive relationship between distance and SVL than juveniles with biological mothers, which dispersed similarly across all body sizes. There was no significant effect of sex on movement probability or distance ($P > 0.5$; Supplementary Material, Supplementary Table 3).

Field dispersal

I recaptured 23 of 160 (14.4%) juveniles released into the field. One of these juveniles was an LDD (245 m), moving more than 57 times the average distance the rest of the lizards moved (4.23 m) and more than 11 times the distance of the next furthest movement. However, this dispersal distance is well within the range observed for naturally moving individuals in the same (Davis et al. 2011) and another population (Zweifel and Lowe 1966). All recaptured juveniles were caught at least once during winter collections up to 2.5 years after their birth, except for one juvenile, which was only caught in the summer at 1 year of age.

I found that a larger proportion of juveniles in foster environments dispersed than juveniles released with biological siblings ($\chi^2 = 4.21$, df = 21, $P = 0.040$). None of the recaptured individuals released with biological siblings moved further than 4 m (Figure 4), and at least one was found under
the same log where released a year earlier. Again, there was no effect of sex ($P = 0.86$). Juveniles released with foster siblings also dispersed further than those released with biological siblings (Figure 4; Likelihood ratio test of fitted geometric distributions, $P < 0.001$; $P = 0.12$ when LDD excluded).

**Field aggregation**

I found that lizards released with kin were more likely to join aggregations and that these aggregations were larger than those joined by lizards released with unrelated individuals. A larger proportion of juveniles aggregated when placed with biological siblings than juveniles released with foster siblings (Figure 5a; $\chi^2 = 4.38$, df = 20, $P = 0.0363$). Juveniles released with biological mothers also joined aggregations about 3 times as large as the groups joined by lizards released with foster mothers (Figure 5b; Wilcoxon signed-rank test, $W = 2$, $P = 0.015$). Although juveniles released with kin commonly aggregated specifically with related individuals, it is also of note that I did find 3 fostered juveniles still aggregated with their foster mothers on recapture.

**DISCUSSION**

Using a cross-fostering experiment, I found that juvenile lizards placed with unrelated individuals were generally more likely to disperse, traveled greater distances, were less likely to aggregate, and joined smaller aggregations than juveniles released with their genetic relatives. This finding that kin presence actively promotes both philopatry and sociality in juvenile *X. vigilis* is consistent with the predictions of kin cooperation and suggests that kin sociality in *X. vigilis* is not simply a by-product of limited dispersal. Below, I discuss how these results yield insight about the generality and direction of kin effects, how these effects are mediated, and the future study of kin selection.

**Kin effects on dispersal and sociality**

One interesting result of this experiment is that juveniles respond to mother presence in the lab and sibling presence in the field. Both of these effects on juvenile movement are such that kin presence promotes philopatry, but juveniles response appears to be driven by different kinds of kin presence in the 2 tests. This result could have several explanations, but one simple possibility is that juvenile needs change ontogenetically, as juveniles were tested in the laboratory before 2 weeks of age and field-recaptured juveniles were up to 2.5 years old. Maternal presence might be critical to very young juveniles but become a less important indicator of kin environment as the juvenile nears adulthood, perhaps due to generational age differences.

Although direct manipulative tests of kin effects on dispersal are still not common, other studies have also suggested positive effects of kin on philopatry and sociality in a wide variety of systems, including spiders (Jones and Parker 2002), rodents (reviewed in Sherman 1981; Lambin et al. 2001), primates (reviewed in Silk 2002), and birds (Eikenaar et al. 2007; Hatchwell 2009). The ability of kin to promote philopatry and sociality appears to be a widespread common phenomenon across taxa. However, many of these examples also involve a sex bias in dispersal, which I did not find in *X. vigilis* juveniles (or in an expanded data set of 265 recaptured juveniles and adults, see Davis et al. 2011). Theory predicts that sex-biased dispersal often results from inbreeding avoidance (Perrin and Goudet 2001), which may be absent in *X. vigilis*. One explanation for this absence might be high population density combined with considerable genetic

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**Figure 3**

An interaction effect between type of mother present and body size (SVL) on movement distance in juvenile lizards (Poisson GLMM, $z = -2.096$, df = 156, $P = 0.036$) shows different positive relationships between SVL and distance in juveniles with biological mothers (a) than with foster mothers (b). Solid lines show model fit, dashed lines show 95% confidence intervals, and points are randomly jittered along both axes to display overlapping values.

**Figure 4**

Recaptured juveniles dispersed more frequently ($\chi^2 = 4.21$, df = 21, $P = 0.040$) and traveled farther (likelihood ratio test, $P < 0.001$) when released with foster siblings (open circles, $n = 16$) than with biological siblings (crosses, $n = 7$). Gray line denotes the threshold distance for classification as a disperser (see text), points are jittered along the x axis to display overlapping values, and the y axis is broken to allow the display of one LDD.

**Figure 5**

Distance moved (bins) for juveniles with biological mothers (a) versus foster mothers (b). Points are jittered along the x axis to display overlap-
variation present within single populations of this species (Zweifel and Lowe 1966; Davis et al. 2011), ensuring that most lizards are in close proximity to unrelated individuals even when aggregated with kin. Moreover, spring mating and winter social strategies need not be correlated, so dispersal may not be necessary to avoid inbreeding in this species.

Additionally, several studies have found an effect of body size on dispersal similar to that which I found in the laboratory dispersal test. Larger dispersers are generally more successful (e.g., male badgers, Woodroffe et al. 1995), but I failed to find this effect in field-recaptured juveniles. This result could be due to either the relatively small number of juveniles I recaptured in comparison with the number I tested in the lab or the limited variation in body size of juveniles, both of which might reduce statistical power of detecting an effect of body size if present.

Undoubtedly, both competitive and cooperative processes co-occur in species with kin sociality. One extension of kin effect tests that can evaluate the relative importance of the 2 is to quantify resource competition, which could be addressed in X. vigilis by manipulating both log quality and kin in a 2-way factorial design. Indeed, recent results of the interaction between the kin and resources in wasps suggested that kin presence may have greater influence on dispersal choices than limited resources (Giron et al. 2004; see Baglione et al. 2006). More tests of this nature would be an excellent way to determine the ubiquity, strength, and direction of kin effects across systems.

Mediation of kin effects

One important implication of these results involves the mechanism by which kin affect juvenile dispersal and sociality. The main distinction centers on whether juvenile X. vigilis incorporate kin cues into their decision to leave or stay (auto-instigated) or whether foster mothers and siblings force juveniles into dispersal and isolation (allo-instigated). It is generally thought that kin cues are accumulated by the individual and that the dispersal decision is self-instigated (Aragon et al. 2006), but my study did not test between these 2 possible mechanisms. However, several taxa show aggression that is biased toward unrelated conspecifics (Pennig et al. 1993; Beve et al. 1998; Sinn et al. 2008), and it is easy to envision this aggression paired with tolerance for biological offspring producing the same kin effects as self-instigated dispersal using kin recognition cues. However, I did find a few juveniles aggregated with their foster mothers, which suggests that there is some tolerance of unrelated conspecifics within X. vigilis social groups and that dispersal choices may lie primarily with the juvenile. The best way to identify the mechanism responsible for kin effects on dispersal may be to decouple the behavior of other individuals from the cues used by the juvenile by identifying and isolating the cue itself (often chemosensory, in lizards), but this approach remains intractable for many systems and individuals almost assuredly use multiple cues in assessing the kin environment. Although these 2 mechanisms may not be distinguishable for many species and may well work in concert, it is valuable to recognize that 2 very different processes may account for kin effects found through cross-fostering experiments.

Implications for the study of kin selection

One of the most important results from this study is that limited dispersal alone does not explain the preferential association of kin in this species. As in cooperatively breeding birds (Eikenaar et al. 2007), it appears that these lizards actively choose to remain with their parents and siblings for social aggregation. There could be a number of benefits to social aggregation with kin in this species, especially from the viewpoint of juveniles, including indirect parental care through reduced parental aggression (Sinn et al. 2008) or thermoregulatory benefits in cold winter temperatures. Because these aggregations dissolve each spring and reform each fall (sometimes with the same stable related participants for up to 4 years, Davis et al. 2011), the decision to be social with kin must be made repeatedly even after the original decision to remain philopatric. This occurrence suggests that direct and/or inclusive fitness benefits, paired with a mechanism of kin recognition, are more likely than limited dispersal to account for the maintenance of kin sociality in this species.

Also important to the study of kin selection is the finding that this species represents yet another example of kin effects specifically consistent with kin cooperation. One possible reason for the many empirical examples of kin promoting philopatry in vertebrates may be a sampling bias. Most studies of kin selection are performed in highly social species with intriguing social behavior, especially vertebrates, which tend to be social with kin. It must be noted that a bias of this sort would make kin cooperation seem more common and dominant in relation to competition than it may actually be.

However, there is also evidence of spatial association among philopatric kin even in nonsocial species. This evidence is primarily found in mammals and usually depends on the high-density conditions of saturated habitats (Jannett 1978; Lambin and Krebs 1993; Woodroffe et al. 1995), but its presence does provide support that positive kin effects on dispersal are not limited to obviously social species. If cooperative mechanisms really are the dominant force of kin selection in natural systems, then it may be time to reevaluate how heavily we rely on isolated kin competition mechanisms in theoretical work and renew appreciation for how powerful cooperative forces might be in the evolutionary dynamics of animal species.
SUPPLEMENTARY MATERIAL
Supplementary material can be found at http://www.beheco.oxfordjournals.org/.

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