

# Does social complexity lead to sex-biased dispersal in polygynous mammals? A test on ground-dwelling sciurids

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Mating systems are well known to influence the dispersing sex, but the magnitude of the sex-biased dispersal has not actually been measured, whereas many theoretical predictions have been made. In this study, we tested a new prediction about the coevolution between natal dispersal and sociality from a recent evolutionarily stable strategy (ESS) approach. From a comparative approach, we showed that, in agreement with the model, the male-biased dispersal increases with increasing level of sociality in polygynous ground-dwelling sciurids. In addition, the increase in male-biased dispersal with increasing sociality results from an increase in male dispersal rates, whereas female dispersal rates remain constant, contrary to what is expected from the ESS model. Although the mating system through the level of polygyny could act as a confounding factor, our results strengthen previous work that states that inbreeding avoidance plays a major role in the evolution of dispersal for the most social mammalian species. *Key words:* comparative analysis, ground-dwelling sciurids, mammals, sex-biased dispersal, sociality. [*Behav Ecol* 15:83–87 (2004)]

Natal dispersal of animals is a key process in evolutionary biology, and many studies have focused on its ultimate and proximal causes (for reviews, see Clobert et al., 2001; Johnson and Gaines, 1990). Although inbreeding avoidance, resource competition, and mating system have all been shown to influence sex-specific dispersal rate in mammals, most studies have used a unifactorial approach (mating system: Dobson, 1982; Greenwood, 1980; inbreeding avoidance: Wolff, 1993). The need for a pluralistic approach has often been advocated (Perrin and Mazalov, 2000; Stenseth and Lidicker, 1992). For instance, we do not know how mating system and social structure interact with local resource competition and inbreeding avoidance to determine the observed patterns of natal dispersal.

By applying the approach of evolutionarily stable strategies to the interaction between local competition and inbreeding avoidance, Perrin and Goudet (2001) showed that the level of sociality could strongly affect natal dispersal patterns. The effects of increasing sociality, both for sex-specific natal dispersal rates and for the magnitude of sex-biased natal dispersal, were shown to depend on two main factors: between-sex differences in benefits of kin cooperation and level of inbreeding costs. Benefits of sociality are assumed to occur through cooperation among philopatric relatives in the natal area, whereas dispersers could not benefit from kin cooperation because they joined unrelated individuals. Defined as above, benefits of sociality could be viewed as some of the benefits of philopatry. In polygynous species where males defend access to females, dispersal is male biased because processes affecting males, such as local mate competition (Dobson, 1982; Moore and Ali, 1984) and inbreeding avoidance (Greenwood, 1980; Wolff, 1993), and processes

affecting females, such as higher benefits of philopatry due to their greater parental investment in producing and rearing offspring (Clutton-Brock, 1991), are different. By these criteria, females should thus benefit more than males from kin cooperation in polygynous mammals.

When such a sex difference occurs in the benefits of sociality, Perrin and Goudet (2001) predicted that philopatry of females should be enhanced by the additional social benefits of staying in their natal territory, whereas males should disperse more to avoid inbreeding costs, which are not, in this case, counterbalanced by advantages of kin cooperation. As a consequence, the magnitude of male-biased natal dispersal is expected to increase with increasing sociality and female philopatry, and even more so when inbreeding costs are high for a given level of sociality. An increase in male dispersal rates and a decrease in female dispersal rates with increasing sociality therefore appear to account for the increase in male-biased dispersal in social species.

We conducted a first empirical test of Perrin and Goudet's (2001) model by using polygynous ground-dwelling Sciurids. This group is well suited for such a test because ground-dwelling sciurids show a large range of social structures from solitary species to species that form large, multigenerational social units (see Armitage, 1981; Michener, 1983). In a life-history theory context, such variability in social structure is correlated with other life-history traits such as communicative complexity (Blumstein and Armitage, 1997), proportion of breeding females, age at first reproduction, litter size, and juvenile survival (Blumstein and Armitage, 1998). However, natal dispersal rates have not been integrated in previous analyses, whereas natal dispersal of ground-dwelling sciurids has been well studied by long-term monitoring of several species.

In this study, we tried to answer two questions: (1) Does the magnitude of male-biased natal dispersal increase with increasing sociality as expected from Perrin and Goudet's (2001) model? (2) Does male dispersal and female philopatry increase with increasing sociality?

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**Table 1**  
**Social complexity index (SCI; Blumstein and Armitage, 1997) and natal dispersal rates for the 11 species of ground-dwelling sciurids**

Species	SCI	Natal dispersal rates		References <sup>a</sup>	Methods <sup>b</sup>
		Males	Females		
1- <i>Spermophilus elegans</i>	0.43	0.666	0.548	1	KF + D
2- <i>Spermophilus richardsonii</i>	0.39	0.27	0.10	2	KF
3- <i>Spermophilus beldingi</i>	0.40	0.914	0.6535	3	KF + D
4- <i>Spermophilus columbianus</i>	0.65	0.839	0.202	4–5	KF + D
5- <i>Spermophilus townsendii</i>	0.41	0.577	0.083	6	KF
6- <i>Spermophilus variegatus</i>	0.43	0.777	0.714	7	D
7- <i>Spermophilus tereticaudus</i>	0.48	0.65	0.1875	8	KF
8- <i>Cynomys gunnisoni</i>	1.03	0.955	0.05	9	KF
9- <i>Cynomys ludovicianus</i>	1.12	1	0.383	10	KF + D
10- <i>Marmota monax</i>	0.27	0.909	0.647	11	KF
11- <i>Marmota flaviventris</i>	1.06	1	0.5	12	KF + D

<sup>a</sup> References (sample size, when available, and complementary information are equally provided): 1, Pfeifer, 1982: 36 males/31 females; 2, Michener and Michener, 1977: 26 males/60 females; 3, Holekamp, 1984: means of dispersal rates from two populations, 260 males/400 females; 4, Wiggett and Boag, 1992: 188 females; 5, Wiggett and Boag, 1993: 255 males; 6, Olson and Van Horne, 1998: 26 males/12 females; 7, Johnson, 1981: 9 males/14 females; 8, Dunford, 1977: 17 males/16 females; 9, Hoogland, 1999: 66 males/358 females (male dispersal rate was calculated for potential dispersers at 2 years, whereas female dispersal rate was calculated for yearling females because of sex-difference in age at sexual physiological maturity); 10, Halpin, 1987: 75 males/81 females; 11, Meier, 1992: 11 males/17 females; 12, Armitage, 1991, unpublished data.

<sup>b</sup> Methods used to estimate dispersal rates are provided for each species: “known fates” (KF) refers to estimates based on individual localizations before and after natal dispersal; “disappearance” (D) concerns estimates based on the proportion of individuals that disappear and will be never again relocated in another place. Potential dispersers are defined as the individuals from the original cohorts for whom authors know that they are not dead or they have not lost their mark before the beginning of the dispersal events measurement.

## METHODS

### Data collection

We reviewed the literature for studies that reported natal dispersal rates of the two sexes in ground-dwelling sciurids (ground squirrels, *Spermophilus* spp.; marmots, *Marmota* spp.; and prairie dogs, *Cynomys* spp.). Dispersal rates were defined as the ratio of the number of animals who leave their natal site or social group before their first reproduction to the total number of potential dispersers present in the population (see Table 1 for more details). To define the level of sociality of a species, we used the social complexity index defined and calculated for ground-dwelling sciurids by Blumstein and Armitage (1997). This index of social complexity is derived from relative frequencies of the different age and sex classes that interact in the social group. This continuous index is consistent with the previous classifications of social structure in ground-dwelling sciurids (Armitage, 1981; Michener, 1983) and is expected to more adequately describe the sociality than group size alone (Blumstein and Armitage, 1997).

### Social complexity, sex bias, and dispersal rates

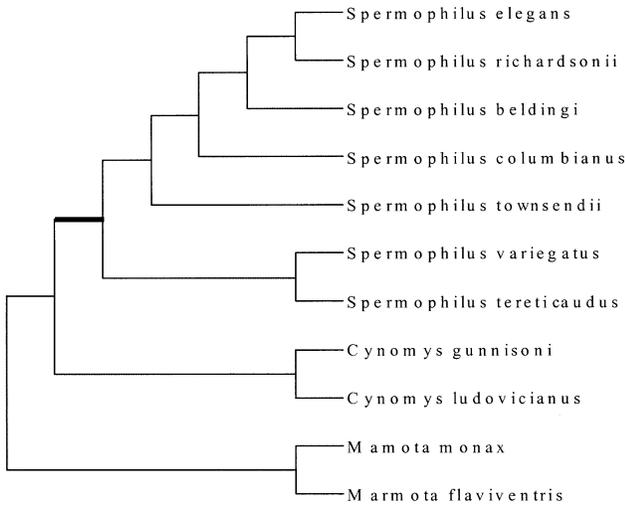
We used the arcsine square-root transformation for normalizing dispersal rates (Sokal and Rohlf, 1981). Sex bias in natal dispersal was calculated as the difference between male and female dispersal rates after arcsine square-root transformation.

We regressed both sex-biased dispersal and sex-specific dispersal rates on the social complexity index. To address such an interspecific analysis, we took into account the non-independence of species because of phylogenetic inertia (Felsenstein, 1985). We used Garland and Ives's method (2000) based on a general least-squares approach (Martins

and Hansen, 1997) using distances among related species, calculated from common ancestry, in a weighted regression. For the analysis, we used the same phylogenetic tree as Blumstein and Armitage (1997, tree A), excluding species for which no dispersal rates were available in the literature (Figure 1). All branch lengths were set to 1 (Purvis et al., 1994). To avoid possible problems with polytomies, branch lengths were fixed at 0.0001 when a polytomy occurred. This numerical artifact is equivalent to a very fast radiation of more than two species or more than two groups of species (Maddison, 1989). We used PDTREE 5.0 software for all analyses (Garland and Ives, 2000). However, the usefulness of phylogenetic comparative methods has been challenged because life-history traits are not systematically correlated with their phylogenetic history (Abouheif, 1999; Björklund, 1997; Price, 1997; Ricklefs and Starck, 1996). We used the bootstrap test for serial independence (TFSI; PI Software, Abouheif 1999) to check for the phylogenetic independence of sex-biased dispersal, for male and female natal dispersal rates, and for the social complexity index. All TFSI were done with 5000 iterations. Following Abouheif (1999), we performed both the conventional approach without taking into account the phylogeny and the phylogenetic comparative approach because results of the TFSI were contrasted among traits of interest (see Results).

## RESULTS

We gathered information on sociality and dispersal rates for 11 species that fulfilled our criteria (2 *Marmota*, 2 *Cynomys*, and 7 *Spermophilus*; Table 1). In all cases, males dispersed more than females. As expected from the model (Perrin and Goudet, 2001), male bias in dispersal rates increased with



**Figure 1**  
Phylogenetic tree of the ground-dwelling sciurids. Polytomy between *Cynomys* spp. and *Spermophilus* spp. is represented by the bold line and is set equal to 0.0001 in the regression analysis.

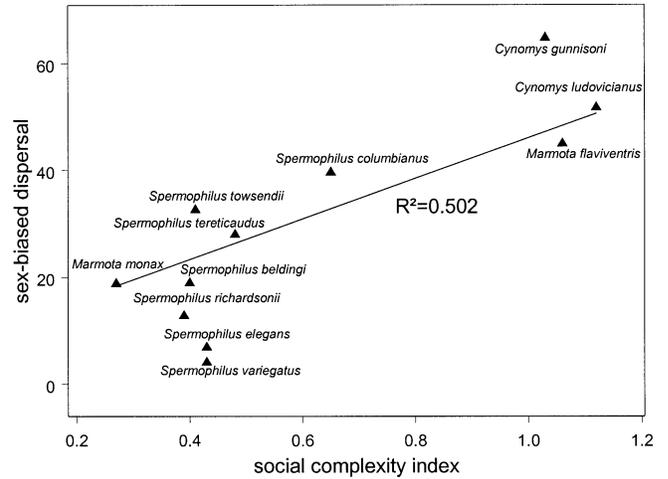
increasing social complexity ( $R^2 = .502$ , one-tailed  $p = .007$ ,  $df = 9$ ; Figure 2) among the 11 species of polygynous ground-dwelling sciurids, after phylogeny was accounted for. Accordingly, males dispersed more when social complexity increased ( $R^2 = .319$ , one-tailed  $p = .035$ ,  $df = 9$ ; Figure 3). However, contrary to what was expected, no relationship occurred between female natal dispersal rates and social complexity ( $R^2 = .02$ , one-tailed  $p = .33$ ,  $df = 9$ ; Figure 3).

TFSI showed that both the male-biased dispersal ( $p = .037$ ) and the male dispersal rates ( $p = .047$ ) were correlated with phylogeny. Contrary to these two traits, female dispersal rates were not correlated with phylogeny ( $p = .387$ ), whereas social complexity index tended to be ( $p = .08$ ). When phylogeny was not accounted for, previous results remained similar for male-biased dispersal ( $R^2 = .72$ ,  $p = .001$ ,  $df = 9$ ), for male dispersal rates ( $R^2 = .51$ ,  $p = .013$ ,  $df = 9$ ), and for female dispersal rates ( $R^2 = .05$ ,  $p = .50$ ,  $df = 9$ ).

**Discussion**

We do not know how variability in the methods used in dispersal measurements contributed to the relationships shown in this study. However, inspection of data (Table 1) revealed no obvious confounding effects. Estimates from “disappearance methods” that may overestimate dispersal rates were not consistently the highest rates. Likewise, estimates from “known fate methods” that may underestimate dispersal rates were not consistently the lowest rates. The absence of confounding effect of method used to assess dispersal allowed us to interpret our results in the light of the evolutionary hypotheses we aimed to test.

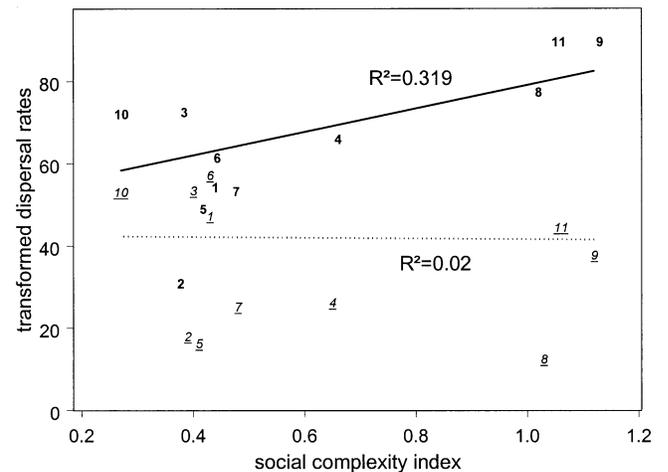
Male-biased dispersal was observed in the 11 species of ground-dwelling sciurids. Such results support the pattern of natal dispersal commonly reported for polygynous mammals (Dobson, 1982; Greenwood, 1980; Wolff, 1993) and predicted by theoretical models (Perrin and Goudet, 2001; Perrin and Mazalov, 1999, 2000). In addition to the well-known influence of mating system on sex-biased natal dispersal of mammals and birds (e.g., Greenwood, 1980), we show here that the level of sociality, reflected by the social complexity index, affects the magnitude of male bias in dispersal rates of polygynous ground-dwelling sciurids, as predicted from the theoretical



**Figure 2**  
Social complexity and sex-biased dispersal (slope  $\pm$  SE:  $37.88 \pm 12.57$ ) in 11 species of polygynous ground-dwelling sciurids, after arcsine square-root transformation of the dispersal rates and taking into account phylogenetic inertia with Garland and Ives’ (2000) method.

model of Perrin and Goudet (2001). Our results show that the increase of the sex-biased dispersal result principally from a significant increase in male dispersal rates with increasing level of sociality; the decrease in female dispersal rates is not significant.

Male dispersal rates were also higher in social species than in nonsocial species considered. At the demographic level, such a result might occur because the turnover of dominant and reproductive adult males would be lower for some social species (yellow-bellied marmot *Marmota flaviventris*, black-tailed prairie dog *Cynomys ludovicianus*; Blumstein and Armitage, 1998) than for non social ones (Belding’s and Richardson’s ground squirrels, *Spermophilus beldingi* and *Spermophilus richardsonii*; Blumstein and Armitage, 1998). As



**Figure 3**  
Relationship between social complexity and sex-specific natal dispersal rates, after arcsine square-root transformation of the dispersal rates for males (slope  $\pm$  SE,  $28.39 \pm 13.81$ ) and for females (slope  $\pm$  SE,  $-9.49 \pm 21.05$ ). Numbers refer to species in Table 1. Bold numbers correspond to data for males; italics and underlined numbers refer to females.

a consequence, opportunistic philopatry of males through occupation of a new vacant territory (Waser, 1988) is more likely in nonsocial than in social species. Thus, the highest male dispersal rates should be observed in the more social species. Such a pattern is reinforced by the non-independence between sociality and mating system in ground squirrels (Armitage, 1981), which could act as a partial confounding factor. Indeed, the levels of both polygyny and sociality are probably positively linked, at least for the beginning of the sociality gradient (i.e., the four first classes in the Michener's [1983] classification). Thus, male local mate competition should increase with the level of sociality and should enhance male dispersal. However, for the most social species with egalitarian polygynous harems (*Cynomys ludovicianus* and *Cynomys gunnisoni*; Michener, 1983), there is no evidence that local mate competition is stronger than in less social species, even if competition remains high in social species (e.g., *Marmota flaviventis*; Armitage 1974). Effects of sociality could then be assessed with a low confounding effect of the mating system in the most social species of the analysis. Unfortunately, we did not find reliable dispersal data for the most social species in the Blumstein and Armitage's (1997) continuum of social complexity (e.g., *Marmota olympus*). We thus do not know what is happening at the high social complexity extremity of continuum. Given the agreement of our results with Perrin and Goudet's (2001) prediction, inbreeding avoidance appears to be the main factor driving the evolution of sex-biased dispersal in social species (Pusey and Wolf, 1996), even if other ultimate factors are likely to play a role (e.g., local resource competition; Dobson and Jones, 1985).

An inbreeding avoidance hypothesis is explicit in the genetic model of Chesser (1991, 1998). This model assumes that a polygynous mating system associated with natal dispersal of all males and philopatry of all females is the socioecological context that best promotes evolution of sociality by allowing a high level of co-ancestry while limiting inbreeding costs. Under Chesser's hypothesis, we should observe the highest male-biased dispersal when the greatest possible level of sociality occurs in polygynous species.

Contrary to what is observed for males, the absence of any relationship between female dispersal rates and sociality does not support Perrin and Goudet's (2001) model, which assumes a decrease in female dispersal rates with increasing social complexity. In polygynous mammals, females alone provide parental care to the young (Clutton-Brock, 1991). Consequently, they invest more than males in offspring production and rearing (Clutton-Brock, 1991). Even if females suffer more than males from inbreeding costs (Greenwood, 1980; Perrin and Mazalov, 2000), it should be more advantageous for them to remain in their natal home range as a result of their knowledge of resource and shelter distribution (Greenwood, 1980, Dobson, 1982). Additional fitness gains of philopatry due to sociality (e.g., kin cooperation) might have been too weak to promote a decrease in already low female dispersal rates in ground-dwelling sciurids. Moreover, our results show that female dispersal rates are more variable than male dispersal rates in both social and nonsocial species (Figure 3).

Because of between-sex differences in parental investment, females should suffer a higher level of local resource competition than males, who are more influenced by local mate competition in polygynous mating systems (Clutton-Brock, 1991). Intraspecific variation in the intensity of local resource competition among related females could thus be more important than intraspecific variation in local mate competition among related males. The expected negative relationship between female dispersal rates and level of sociality predicted by Perrin and Goudet (2001) might

therefore be confounded by intraspecific variation of female dispersal rates. As emphasized by Perrin and Mazalov (2000) and suggested by our results, the level of habitat saturation, which acts on the level of local resource competition among females, must be taken into account when analyzing dispersal rates of the sex that competes for local resources (i.e., females in polygynous mating systems).

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## REFERENCES

- Abouheif E, 1999. A method for testing the assumption of phylogenetic independence in comparative data. *Evol Ecol Res* 1: 895–909.
- Armitage KB, 1974. Male behavior and territoriality in the yellow-bellied marmot. *J Zool* 172:233–265.
- Armitage KB, 1981. Sociality as a life-history tactic of ground squirrels. *Oecologia* 48:36–49.
- Armitage KB, 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. *Annu Rev Ecol Syst* 22: 379–407.
- Björklund M, 1997. Are "comparative methods" always necessary? *Oikos* 80:607–612.
- Blumstein DT, Armitage KB, 1997. Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurids alarm calls. *Am Nat* 150:179–200.
- Blumstein DT, Armitage KB, 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. *Behav Ecol* 9:8–19.
- Chesser RK, 1991. Gene diversity and female philopatry. *Genetics* 127: 437–447.
- Chesser RK, 1998. Relativity of behavioral interactions in socially structured populations. *J Mammal* 79:713–724.
- Clobert J, Danchin E, Dhondt AA, Nichols JD, 2001. *Dispersal: individual, population and community*. Oxford: Oxford University Press.
- Clutton-Brock TH, 1991. *The evolution of parental care*. Princeton, New Jersey: Princeton University Press.
- Dobson FS, 1982. Competition for mates and predominant juvenile male dispersal in mammals. *Anim Behav* 30:1183–1192.
- Dobson FS, Jones WT, 1985. Multiple causes of dispersal. *Am Sci* 126: 855–858.
- Dunford C, 1977. Behavioral limitation of round-tailed ground squirrel density. *Ecology* 58:1254–1268.
- Felsenstein J, 1985. Phylogenies and the comparative methods. *Am Nat* 125:1–15.
- Garland TJ, Ives AR, 2000. Using the past to predict the present: confidence intervals for regression equations in phylogenetic comparative methods. *Am Nat* 155:346–364.
- Greenwood PJ, 1980. Mating systems, philopatry and dispersal in Birds and Mammals. *Anim Behav* 28:1140–1162.
- Halpin ZT, 1987. Natal dispersal and the formation of new social group in a newly established town of black-tailed prairie dogs (*Cynomys ludovicianus*). In: *Mammalian dispersal patterns: the effects of social structure on population genetics* (Chepko-Sade BD, Halpin ZT, eds). Chicago: University of Chicago Press; 104–118.
- Holekamp KE, 1984. Natal dispersal in Belding's ground squirrel (*Spermophilus beldingi*). *Behav Ecol Sociobiol* 16:21–30.
- Hoogland JL, 1999. Philopatry, dispersal, and social organization of Gunnison's prairie dogs. *J Mammal* 80:243–251.
- Johnson K, 1981. Social organization in a colony of rock squirrels (*Spermophilus variegatus*, Sciuridae). *Southwest Nat* 26:237–242.
- Jonhson ML, Gaines MS, 1990. Evolution of dispersal: theoretical models and empirical tests using birds and mammals. *Annu Rev Ecol Syst* 21:449–480.
- Maddison WP, 1989. Reconstructing character evolution on polytomous cladograms. *Cladistics* 5:365–367.

- Martins EP, Hansen TF, 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *Am Nat* 149:646–667.
- Meier PT, 1992. Social organization of woodchucks (*Marmota monax*). *Behav Ecol Sociobiol* 31:393–400.
- Michener GR, 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. In: *Recent advances in the study of mammalian behavior* (Einsenberg JF, Kleiman DG, eds). Stillwater, OK: American Society of Mammalogists Special Publication no. 7; 528–572.
- Michener GR, Michener DR, 1977. Population structure and dispersal in Richardson's ground squirrels. *Ecology* 58:359–368.
- Moore J, Ali R, 1984. Are dispersal and inbreeding avoidance related? *Anim Behav* 32:94–112.
- Olson GS, Van Horne B, 1998. Dispersal patterns of juvenile Townsend's ground squirrel in southwestern Idaho. *Can J Zool* 76:2084–2089.
- Perrin N, Goudet J, 2001. Inbreeding, kinship, and the evolution of natal dispersal. In: *Dispersal: individual, population and community* (Clobert J, Danchin E, Dhondt AA, Nichols JD, eds). Oxford: Oxford University Press; 127–146.
- Perrin N, Mazalov V, 1999. Dispersal and inbreeding avoidance. *Am Nat* 154:282–292.
- Perrin N, Mazalov V, 2000. Local competition, inbreeding, and the evolution of sex-biased dispersal. *Am Nat* 155:116–127.
- Pfeifer S, 1982. Disappearance and dispersal of *Spermophilus elegans* juveniles in relation to behavior. *Behav Ecol Sociobiol* 10:237–243.
- Price T, 1997. Correlated evolution and independent contrasts. *Phil Trans R Soc Lond B* 352:519–529.
- Purvis A, Gittleman JL, Luh HK, 1994. Truth or consequences: effects of phylogenetic accuracy on two comparative methods. *J Theor Biol* 167:293–300.
- Pusey A, Wolf M, 1996. Inbreeding avoidance in animals. *Trends Ecol Evol* 11:201–206.
- Ricklefs RE, Starck JM, 1996. Applications of phylogenetically independent contrasts: a mixed progress report. *Oikos*, 77:167–172.
- Sokal RR, Rohlf FS, 1981. *Biometry*. New York: W.H. Freeman.
- Stenseth NC, Lidicker WZ, 1992. *Animal dispersal: small mammals as a model*. London: Chapman and Hall.
- Waser PM, 1988. Resources, philopatry, and social interactions among mammals. In: *The ecology of social behavior* (Slobodchikoff CN, eds). San Diego, California: Academic Press; 109–130.
- Wiggett DR, Boag DA, 1992. The resident fitness hypothesis and dispersal by yearling female Columbian ground squirrels. *Can J Zool* 70:1984–1994.
- Wiggett DR, Boag DA, 1993. The proximate cause of male-biased natal emigration in Columbian ground squirrels. *Can J Zool* 71:204–218.
- Wolff JO, 1993. What is the role of adult in mammalian juvenile dispersal? *Oikos* 68:173–175.