

The evolution of vocal alarm communication in rodents

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On encountering a predator, many species emit potentially risky vocalizations known as alarm calls. We evaluated the relative importance of two adaptive hypotheses on the evolution of calling: (1) communicating to predators, which may function by deterring pursuit and hence increasing individual survival, and (2) an alternative nepotistic hypothesis for alarm calling whereby callers obtain direct and indirect fitness by warning relatives. Focusing on 209 species of rodents, we found significant associations between diurnality and alarm calling, living socially and alarm calling, and diurnality and sociality. Diurnality, however, accounted for nearly three times as much variation in whether or not a species alarm called than did sociality. Phylogenetic tests revealed that the evolution of diurnality preceded the evolution of alarm calling, and that the evolutions of diurnality and sociality were unrelated. Our results are consistent with the hypothesis that alarm communication evolved to communicate to predators. If so, then nepotistic benefits, although important for the maintenance of alarm calling in some rodents, may be relatively less important in its evolution. *Key words*: alarm calling, evolution, rodent behavior. [*Behav Ecol*]

Why animals emit potentially risky alarm calls has puzzled evolutionary biologists for decades (Klump and Shalter, 1984; Maynard Smith, 1965), and understanding the adaptive utility of alarm communication has been influential in explaining the evolution of social behavior through kin selection (Keller and Reeve, 2002). Since Sherman's (1977) and Dunford's (1977) classic studies that demonstrated nepotistic benefits from calling in ground squirrels, others have found evidence that animals obtain both direct and indirect fitness (Brown, 1987) by emitting potentially risky alarm vocalizations (Blumstein et al., 1997; Hoogland, 1995; Schwagmeyer, 1980). It is therefore surprising that the evolutionary origin of alarm calling has remained virtually unexplored.

The methods of studying current adaptive utility are, theoretically, straightforward and involve correlative and experimental components: (1) hypothesize an adaptive function, (2) search for correlations between variation in trait expression and evolutionary fitness, and (3) manipulate trait expression to demonstrate causality (Tinbergen, 1963; Tinbergen et al., 1962). Demonstrating the initial conditions favoring the evolution of a trait are, however, explicitly correlative. Evolutionary questions, such as these, are studied by using the comparative method in which the distribution of traits among many species is identified and hypotheses about coevolution are formally tested (Brooks and McLennan, 1991; Harvey and Pagel, 1991; Maddison and Maddison, 2001). Evolution is cumulative, and the conditions favoring the initial evolution of a trait and its subsequent maintenance need not be identical (Darwin, 1859; Reeve and Sherman, 1993). The challenge to understanding the initial evolutionary function is to generate hypotheses and variables suitable for comparative analysis that test complementary adaptive hypotheses. There are two major nonexclusive hypotheses to explain the current adaptive utility of alarm calling: communicating to predators to discourage pursuit (Hasson, 1991),

and communicating to conspecifics to warn them about danger (Maynard Smith, 1965; Zuberbühler et al., 1999).

Abundant evidence suggests that animals reduce risk to themselves when emitting alarm signals (Blumstein, 1999; Hasson, 1991) and, under certain circumstances, do not produce alarm signals because by doing so they would make themselves even more vulnerable to predators (Caro, 1995). Because hunting success often requires an element of surprise, individuals may alarm call to alert the potential predator that it has been detected. Alarm signals may also transmit information to the predator about the caller's physical ability to elude capture or defend itself (Fitzgibbon and Fanshawe, 1988). By deterring a predator's attack, a calling individual gains personal fitness benefits. If we assume that alarm calling evolved to communicate to predators, we would expect that calling individuals would try to minimize their risk while calling. One way to do so would be to vocalize only when it is possible to locate and track predators visually, because visual predator detection may more accurately assess the risk of predation (Lima, 1988a,b). Because there is evidence in several species that prey visually assess the relative risk of predation and only call when they are not subjected to excessive risk (Blumstein and Armitage, 1997; Wolff, 1980), we would predict alarm calling species to be diurnal, and alarm calling to be rare or absent in nocturnal species, which are constrained in their ability to reliably assess and manage predation risk.

The intrinsic risk of alarm calling may also be offset by the potential for nepotistic benefits (Sherman, 1977; 1980). Instead of, or in addition to, communicating to the predator, a caller may warn conspecifics about danger. If relatives flee to safety in response to a call, the caller gains inclusive fitness through their survival. If alarm calling evolved via nepotism, we would expect to see social species (particularly those living near kin) more likely to call than are nonsocial species.

Rodents provide an excellent model system in which to study the evolution of alarm calling because they vary in the degrees to which they are vocal, diurnal, and social. We summarized these data for 209 species of rodents from 24 different families, and used both nonphylogenetic and phylogenetic tests to investigate the associations between the evolution of diurnality, living socially, and alarm calling.

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METHODS

Developing the comparative data set

To sample all rodents, including those that are known to alarm call and those that are not, species account numbers one through 702 in *Mammalian Species* (references are available in Appendix and *Neotropical Rainforest Mammals* (Emmons, 1997) were examined. We defined alarm calling as noises, usually loud, emitted when a predator was detected. For most of the 209 species included in our final analyses, our references specified that animals emitted alarm calls in the presence of predators. When we had good descriptions of the sounds a particular species made in a variety of contexts and there was no mention of alarm calls, or the sources specifically stated that the species was not known to alarm call, we classified it as not alarm calling. When we had little or ambiguous data regarding the sounds a species made, we considered it unknown and removed it from the data set. "Fear screams" or other defensive noises (e.g., tooth chattering) were not considered alarm calling. Species for which we were unsure of the context or those species described as making noises when held by a human were not categorized as alarm calling. Data about activity patterns, sociality, vocalizations, and the context in which vocalizations were emitted were summarized. A variety of guides and reviews (references are available as in the Appendix) described additional species of rodents that emit alarm calls, as well as data to fill in gaps about activity patterns, sociality, and vocalizations. Experts were consulted (see Acknowledgments) to provide additional data on several species.

We conducted two complementary analyses. First, for our data set of 209 species, those reported to be active at least 50% of the day were scored as diurnal; those active mostly at night, as nocturnal. Second, we modified our definition of diurnality. In our strict definition, we classified a species as diurnal if it was never reported to be active at night. This reduced our sample size to 156 species. Species likely to be found near kin, because either they lived in family groups or they lived in colonies or foraged in aggregations were scored as social. Animals reported only to be found solitarily or in pairs, or those reported to be territorial and noncolonial, were scored as not social. By defining sociality this way, we classify as social species such as solitary, but colonial, ground squirrels (*Spermophilus* spp.) that have been the subject of many studies of the adaptive significance of calling, and we classify as nonsocial species such as muskrats (*Ondatra zibethicus*) and North and South American porcupines (*Erethizon dorsatum* and *Coendou* spp.) that inevitably include species with some degree of maternal care.

Nepotistic benefits from calling could have evolved or be maintained by the benefits from warning vulnerable offspring during a period of parental care (Dawkins, 1979; Hamilton, 1964a,b). However, in some squirrels (Swaigood et al., 1999), mothers direct antipredator behavior and vocalizations specifically toward predators during the time when they care for vulnerable and unresponsive offspring. Species reported to alarm call in the presence of a predator or other disturbances were scored as alarm calling, whereas species were scored as not alarm calling if there were vocalization data, but alarm calling was not reported.

Developing the phylogeny

By using the phylogeny outlined in McKenna and Bell (1997), which updates that of Simpson (1945), we classified to genus the 209 species for which we had complete and unambiguous data. This resolved the majority of genera that were represented by only one or two species. Those genera with more than two

species remained as unresolved polytomies; many were subsequently resolved by using species-level phylogenetic hypotheses proposed in various studies. Typically, only a single additional phylogeny was sufficient to resolve the species within a genus. The following criteria were applied, in this order, to resolve any genus-level polytomies: (1) molecular hypotheses were used over morphological hypotheses; (2) more recent hypotheses were used over less recent hypotheses; and (3) all else being equal, hypotheses constructed by using parsimony methods were given priority, with consensus between equally parsimonious trees being the most desired. We also explored the effect that two recent molecular phylogenies of holarctic ground squirrels (Harrison et al., 2003; Herron et al., 2004) had on our main results by modifying our tree where appropriate and rerunning all analyses.

Details on phylogeny development

1. *Sciurus*: Two molecular hypotheses (Oshida and Masuda, 2000), using parsimony and likelihood methods. Both hypotheses follow the same structure, but the likelihood method further resolves a polytomy of four species.
2. *Marmota*: Two molecular hypotheses using parsimony (Kruckenhauser et al., 1999) and then likelihood methods (which further resolves a polytomy of three of the species; Steppan et al., 1999).
3. *Spermophilus*: Molecular hypothesis using parsimony methods (Kruckenhauser et al., 1999) and a compiled hypothesis (Blumstein and Armitage, 1998).
4. *Cynomys*: Compiled hypothesis (Blumstein and Armitage, 1998).
5. *Tamias*: Molecular hypothesis using strict consensus methods (Piaggio and Spicer, 2001).
6. *Neotoma*: Two molecular hypotheses using strict consensus methods (Hayes and Harrison, 1992) and parsimony methods (Shibley et al., 1990).
7. *Peromyscus*: Molecular hypothesis using parsimony methods (Hogan et al., 1997).
8. *Reithrodontomys*: Two molecular hypotheses using parsimony methods (Bell et al., 2001) and a phenogram (Nelson et al., 1984).
9. *Microtus*: Two molecular hypotheses using consensus and likelihood methods (Conroy and Cook, 2000). Both hypotheses follow the same structure, but the likelihood methods further resolve a large polytomy.
10. *Gerbillurus*: Molecular hypothesis using parsimony methods (Qumsiyeh et al., 1991).
11. *Rattus*: Molecular hypothesis using UPGMA methods (Baverstock et al., 1986).
12. *Notomys*: Morphological hypothesis using parsimony methods (Watts et al., 1992).
13. *Geomys*: Two molecular hypotheses using consensus and neighbor-joining methods (Jolley et al., 2000). Both hypotheses follow the same structure, but the joining-joining methods further resolve a large polytomy.
14. *Pappogeomys*: Redrawn morphological hypothesis (DeWalt et al., 1993; Russell, 1968).
15. *Perognathus*: Molecular hypothesis using parsimony methods (Riddle, 1995).
16. *Chaetodipus*: Molecular hypothesis using likelihood methods (Riddle et al., 2000).
17. *Dipodomys*: Morphological phenogram. For the resolution of most of the species within *Dipodomys* spp., we chose to use a morphologically based hypothesis (Carrasco, 2000) over a molecularly based hypothesis (Mantooth et al., 2000) from the same year because the morphological tree was more complete and included many more species from this genus. Nonetheless, both

Table 1
Associations between diurnality and alarm calling, sociality and alarm calling, and diurnality and sociality

Diurnal	Alarm call		Social	Alarm call		Diurnal	Social	
	No	Yes		No	Yes		No	Yes
“Liberal” definition of diurnality*								
No	55	25	No	46	40	No	47	33
Yes	18	111	Yes	27	96	Yes	39	90
“Strict” definition of diurnality†								
No	37	15	No	27	36	No	32	20
Yes	5	99	Yes	15	78	Yes	31	73

* All *p*-values < 0.0001; † all *p*-values < 0.0004.

sources agreed on the placement of all but one of the species of *Dipodomys*.

18. *Ctenomys*: Molecular hypothesis using parsimony methods (Slamovits et al., 2001).
19. *Proechimys*: Molecular and morphological hypothesis grouping two species separate from the others (Gardner and Emmons, 1984).

Testing the comparative hypotheses

Fisher’s Exact tests and logistic regression analyses were used to determine if the presence or absence of alarm calling was influenced by activity pattern or sociality. *P* values < .05 were considered significant, and *p* values from .05–.10 were marginally significant. Because such a species-based analysis cannot identify the directionality of trait evolution, and such an analysis is potentially confounded because it does not account for phylogenetic nonindependence between closely related species (Harvey and Pagel, 1991), two phylogenetically based analyses (run with our phylogeny and a one modified based on data reported in Herron et al., 2004) were also used to study the evolution of alarm calling in rodents.

The concentrated changes test (Maddison, 1990) was used to determine the likelihood that the evolution of alarm calling was concentrated on portions of the phylogenetic tree in which diurnal species or in species likely to be found near kin were present. The test requires a fully resolved phylogeny, hence the random resolve option in MacClade version 4.03 (Maddison and Maddison, 2001) was used to resolve any remaining polytomies. The three dichotomous traits were optimized onto

Table 2
Results of four logistic regression analyses conducted on species values

Dependent variable	Independent variable(s)		
	Diurnal <i>p</i>	Social <i>p</i>	<i>R</i> ²
“Liberal” definition of diurnality			
Alarm call	<.0001	—	.247
Alarm call	—	<.0001	.082
Alarm call	<.0001	.0031	.280
Social	<.0001	—	.059
“Strict” definition of diurnality			
Alarm call	<.0001	—	.436
Alarm call	—	.0002	.074
Alarm call	<.0001	.149	.447
Social	.0001	—	.069

Table 3
Results of contingent states test

“Liberal” definition of diurnality

Independent variable state	Dependent variable state						
	ACCTTRAN			DELTRAN			
	Alarm call			Alarm call			
	0->0	0->1	<i>p</i>	0->0	0->1	<i>p</i>	
Diurnal	No	107	8	.0247	117	9	.0018
	Yes	28	8		30	11	
Social	No	87	6	.0549	91	7	.0290
	Yes	48	10		56	13	
Social				Social			
	0->0	0->1	<i>p</i>	0->0	0->1	<i>p</i>	
Diurnal	No	88	11	.8202	90	10	.6321
	Yes	73	11		65	10	

“Strict” definition of diurnality

Independent variable state	Dependent variable state						
	ACCTTRAN			DELTRAN			
	Alarm call			Alarm call			
	0->0	0->1	<i>p</i>	0->0	0->1	<i>p</i>	
Diurnal	No	185	3	<.0001	179	2	.0014
	Yes	36	8		30	5	
Social	No	77	6	.207	79	5	.112
	Yes	144	5		130	2	
Social (strict parsimony)				Social			
	0->0	0->1	<i>p</i>				
Diurnal	No	57	10	.1420			
	Yes	50	3				

p values significant after a Bonferroni correction are in bold. All tests were two-tailed.

the resolved tree to reconstruct the ancestor states for each. In some instances, strict parsimony was not able to fully resolve the reconstructions. Thus, ACCTTRAN and DELTRAN algorithms were applied to each character tree, resulting in a total of six ancestor state reconstructions. The ACCTTRAN algorithm accelerates changes in traits toward the root of the tree, maximizing early gains and forcing early subsequent reversals. The DELTRAN algorithm, on the other hand, delays changes in traits away from the root, thus maximizing parallel changes (Maddison and Maddison, 2001).

The large number of species prevented the use of the concentrated changes test for calculating the exact probability of trait distributions. Instead, the “actual changes” simulation option was used for 10,000 replicates to estimate *p* values for each reconstruction. Also, to account for incorrect resolutions of the ancestor state, simulations were run with the “either ancestral” option selected. To minimize the possibility of falsely interpreting results as significant, a conservative approach was maintained in two ways. First, a Bonferroni correction was applied to the critical *p* value for hypotheses tested by using both ACCTTRAN and DELTRAN reconstructions (new *p* critical .05/2 = .025). Second, fewer and as many gains in the distinguished character, as well as fewer than, as many, or more losses in the distinguished character than

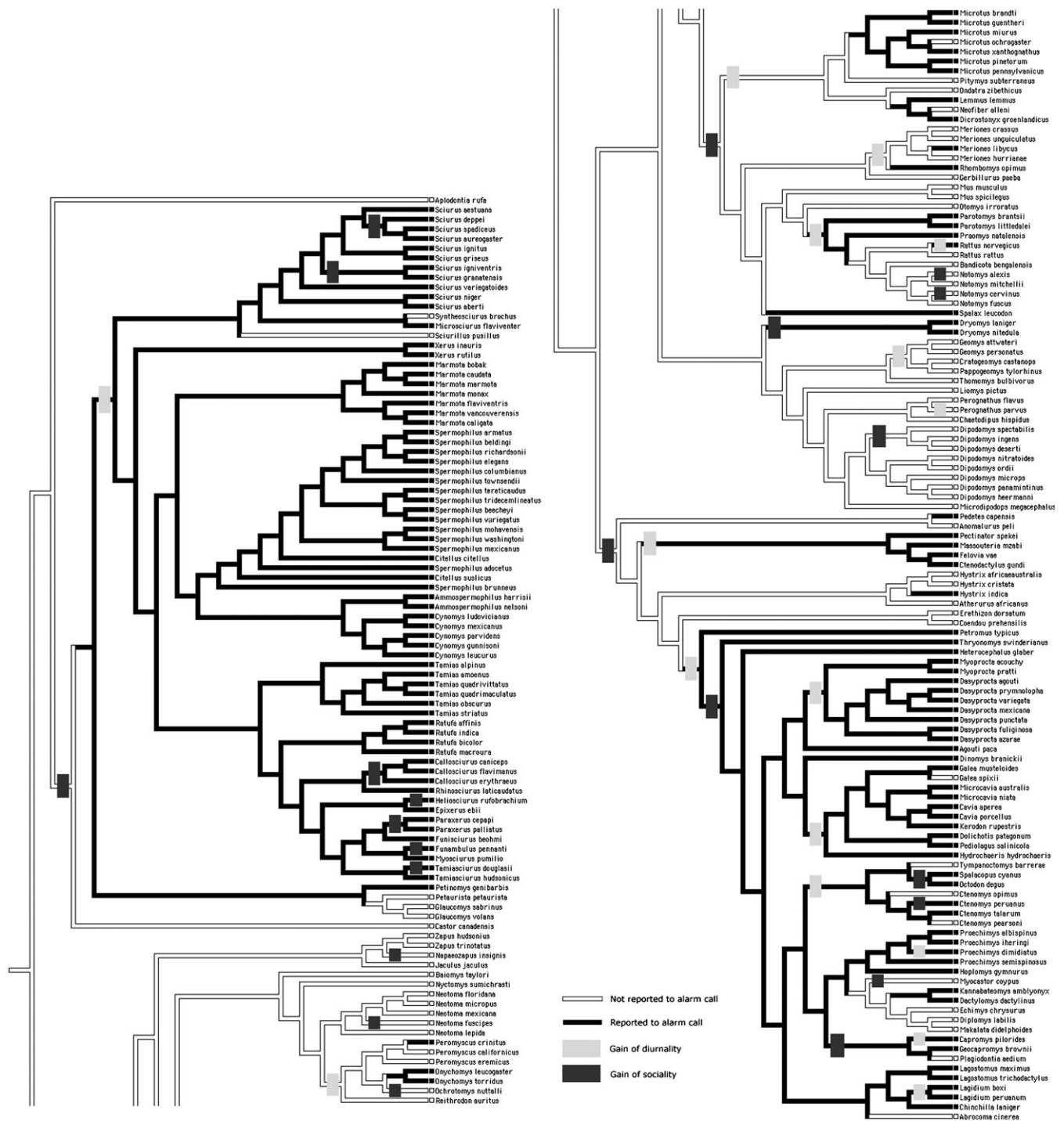


Figure 1 ACCTRAN reconstruction of the evolution of vocal alarm communication in 209 rodent species (ACCTRAN resolution; black squares and bars indicate alarm calling present, white squares and bars indicate alarm calling absent). Reconstructions (ACCTRAN) of the evolutionary origins of diurnality (light bars) and sociality (dark bars) are overlaid on the alarm calling phylogeny that is formally evaluated using the contingent states tests (results reported in Table 3).

actually counted in our analyses, were used when calculating the *p* value in MacClade.

Although the concentrated changes test allowed comparisons between the distributions of two traits on a phylogenetic tree (Swofford and Maddison, 1987), the contingent states test (Sillén-Tullberg, 1993) allowed the use of the phylogenetic reconstruction of characters to ask whether the

transition in one character from zero to one or from one to zero, or the lack of a transition, is equally likely to occur under either state of another character. Thus, it indicated the likelihood that the evolutionary origin of a given trait preceded the evolution of another trait. The main assumption involved is that each branch has an equal probability of state transition. To understand the directionality of the evolution

of the three traits, a series of pair-wise contingent states tests using CoSta version 1.03 (Lindenfors, 1999) were performed for each reconstruction. p values less than the Bonferroni-corrected .025 were interpreted as significant, and $p < .05$ as marginally significant.

RESULTS

Using Fisher's Exact tests, we found significant associations between diurnality and alarm calling, living socially and alarm calling, and diurnality and sociality (Table 1). Diurnality, however, accounted for three to six times as much variation in whether or not a species alarm called than did sociality (Table 2). Logistic regression analyses also allowed us to study the independent influence of diurnality and demonstrated that both diurnality and sociality may explain significant variation in whether or not a species alarm called. However, being diurnal was relatively more important in explaining the extant pattern of alarm calling in rodents (Table 2), a finding that became even stronger when we used a more strict definition of diurnal.

In both data sets (i.e., the 209 species versus 156 species data sets), using the concentrated changes test, we found that both ACCTAN ($p < .001$) and DELTRAN ($p < .0001$) reconstructions revealed significantly more species evolving alarm calling on branches of the tree exhibiting diurnality than would be expected by chance. Alarm calling was also significantly more likely to have evolved on branches of the tree exhibiting sociality (ACCTAN, $p < .0001$; DELTRAN, $p < .0001$). In addition, a significantly greater number of social species was concentrated on branches of the tree characterized by diurnality (ACCTAN, $p < .0001$; DELTRAN, $p < .0001$).

The contingent states test allowed us to identify the directionality of this pattern (Table 3). In both ACCTAN (Figure 1) and DELTRAN reconstructions, diurnality preceded the evolution of alarm calling. When we used ACCTAN reconstructions, sociality did not precede the evolution of alarm calling. In contrast, DELTRAN reconstructions revealed a tendency for sociality to precede the evolution of alarm calling. For both ACCTAN and DELTRAN reconstructions of character states, species that were diurnal were not more likely to evolve sociality.

DISCUSSION

The results of our analyses are consistent with the hypothesis that the evolution of diurnality preceded the evolution of alarm calling in rodents. Overall, sociality also appeared to be associated with the evolution of alarm calling; however, the results of the contingent states tests suggested that species that had evolved sociality were, at most, only marginally more likely to evolve alarm calling.

Although both diurnal and nocturnal animals have sensory capabilities that function well during their respective periods of activity, vision is a key modality to accurately assess and dynamically track predation risk (Lima, 1988a,b). Because these tests all indicated that the evolution of diurnality preceded the evolution of alarm calling, and because prior evidence that prey alarm call only when there is sufficient light to detect and track predators (Blumstein and Armitage, 1997; Wolff, 1980), we suggest that alarm calling may have evolved as a means of communicating to predators. If information about a caller's fitness and state of alertness is transmitted to a potential predator through alarm calling, the caller is likely to discourage pursuit and increase the chance of its survival (Blumstein, 1999; Cresswell, 1994; Fitzgibbon and Fanshawe, 1988; Hasson, 1991). Such detection signaling may be the original function of alarm communication in rodents.

In certain species, alarm calling may also have independently evolved to communicate to conspecifics to warn them of danger. In these cases, the inherent risk of alarm calling may be offset by the potential for nepotistic fitness benefits (Dunford, 1977; Sherman, 1977). Our results cannot exclude the hypothesis that the evolution of calling to warn vulnerable offspring (see Blumstein et al., 1997) was possible only once the safety associated with diurnality evolved. However, if the primary function of calling was to warn vulnerable offspring, we would expect that virtually all diurnal species should alarm call because all have vulnerable offspring at some point of their lives. That they do not suggests, to us, that something else might be important. In addition, paternal care in mammals is not widespread, but males of many species alarm call. Available data do not permit a detailed analysis of sex differences in alarm calling, but the observation that males of nonsocial species call (Burke da Silva et al., 1994) may provide additional evidence against the necessity of a nepotistic origin of calling.

Within this phylogenetic hypothesis, we see certain species that have evolved diurnality, alarm calling, and sociality but subsequently reverted back to a nocturnal lifestyle while retaining alarm calling. Although the initial evolution of alarm calling in these species may have required the evolution of a diurnal activity pattern, alarm calling may subsequently be maintained by the current adaptive utility of social, nepotistic benefits.

The nonphylogenetic analyses and the phylogenetically based concentrated changes test both indicate an association between sociality and diurnality, but they do not specifically test for directionality. The contingent states test, however, reveals that diurnality did not directly lead to the evolution of sociality. This finding eliminates a potential indirect pathway for the evolution of alarm calling; species that evolved diurnality were not more likely to evolve sociality and then, subsequently, evolve alarm calling. Instead, the evolution of diurnality appears to be predominantly and independently responsible for evolution of alarm calling in rodents. Thus, although there are two conceivable pathways to the evolution of alarm calling, surprisingly, given the importance of its adaptive utility, sociality may be of secondary importance in rodents.

APPENDIX

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