The adaptive significance of coloration in lagomorphs

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Lagomorph pelage coloration was matched to habitat type, geographical region, altitude and behaviour to explore the adaptive significance of coloration patterns in this little-studied order of mammals. Analyses were conducted with and without taking phylogeny into account. The former analyses were based on a weighted, phylogenetic supertree for all extant species of lagomorphs that we constructed using morphological and molecular data from 146 papers in the literature. Although our analyses represent an initial, somewhat crude investigation, several clear trends are evident. First, overall body coloration across lagomorphs tends to match the background as shown for pale and red coloration and perhaps seasonal pelage change. The case for countershading being a method of concealment is far less strong. Second, ear tips appear to have a communicative role since they are conspicuous in many different habitats. Third, hypotheses for tail tips having a communicative role, for extremities being dark for physiological reasons, and for Gloger's rule received only partial support. © 2003 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2003, **79**, 309–328.

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INTRODUCTION

For over a century, the adaptive significance of colour patterns in mammals has intrigued biologists (Poulton, 1890; Beddard, 1892; Selous, 1908; Hingston, 1932; Dice & Blossom, 1937). Detailed accounts of species' natural histories have pointed to the importance of camouflage, communication and physiological processes as evolutionary causes for coloration patterns in mammals. Cott (1940) explored four mechanisms contributing to an animal's concealment: general colour resemblance, variable colour resemblance, obliterative shading, and disruptive coloration. General colour resemblance (or 'background

matching') refers to situations in which an animal's coloration generally resembles that of its surroundings (Cott, 1940; Kiltie, 1989). Variable colour resemblance occurs when an animal's coloration alters with its changing surroundings. In some mammals, this colour change occurs seasonally. For example, some mammals that live in regions subject to seasonal snowfall (e.g. mountain hares, *Lepus timidus*) moult into a white pelage in winter, presumably to blend in with the white environment. Obliterative shading, or 'countershading' (Thayer, 1909), refers to pelage coloration where an animal sports a ventral surface lighter than its dorsum, which is thought to counteract the dark shadows cast upon the animal's lower body by the sun (Kiltie, 1988). Thayer (1909) proposed that by minimizing shadows, countershading disguises the animal's three-dimensional form giving the perception that it is a flat, inconspicuous object. Another mechanism for crypsis, disruptive coloration, occurs when distinct lines or marks act to break up the outline of an animal, disguising its form. A possible example in

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lagomorphs comes from the Sumatran rabbit (*Nesolagus netscheri*) which displays striking dark stripes over its shoulders and across its back (Surridge *et al.*, 1999).

Coloration may also play a role in communication. For example, some species, such as the arctic hare (*Lepus arcticus*), moult into a white pelage in winter but retain their conspicuous black ear tips. It is possible that these black ear tips are used for signalling since Holley (1993) has argued that European hares (*Lepus europaeus*) signal to foxes (*Vulpes vulpes*) that they have seen them by standing upright with ears held erect. Similarly, conspicuous white or dark tails may be used to signal to predators or to conspecifics since they are prominent when viewed from behind during flight. For example, Poulton (1890) quotes A. R. Wallace as suggesting that the rabbit's white tail shows conspecifics the way to a burrow.

Coloration may also be related to physiological processes. As examples, the presence of dark coloration on ear tips and tails in many mammals could be related to conditions associated with low temperatures, and Gloger's rule states that dark pelages are found in moist, warm habitats, although the underlying mechanism for this association remains unclear (Gloger, 1833; Huxley, 1942).

Recently, research on the evolutionary mechanisms underlying mammalian coloration has been placed on more rigorous footing in regards to the Lagomorpha (Stoner *et al.*, in press) and the Carnivora (Ortolani & Caro, 1996; Ortolani, 1999), but these advances are necessarily limited in scope and our understanding of the adaptive significance of coloration in other mammals remains rudimentary. In an attempt to provide additional comparative knowledge on this topic and broaden the empirical database, we examined the adaptive function of pelage coloration in Lagomorpha, the mammalian order composed of rabbits, hares and pikas. In particular, we examined the role of background matching, variable colour resemblance (seasonal dimorphism in colour), countershading, and ear and tail coloration in these species by testing predicted associations between these coloration patterns and ecological variables. We performed these tests using both non-parametric statistics and methods that correct for similarity due to common ancestry. The latter tests were based on a consensus phylogeny that we constructed by combining data from taxonomic and phylogenetic studies from the past 100 years using the technique of 'supertree construction' (*sensu* Sanderson, Purvis & Henze, 1998; see below). Thus our study provides the first consensus phylogenetic tree for Lagomorpha and provides tests of hypotheses concerning the adaptive significance of coloration patterns from a comparative perspective. Hitherto such hypotheses have been based primarily on anecdotal observations.

METHODS

SPECIES

The systematics of the Lagomorpha remain controversial (Angermann *et al.*, 1990). Although the monophyly of the order is reasonably certain (Novacek, 1992), its relationship to the other mammalian orders and internal relationships are contentious or poorly studied (Novacek, 1992; Hoffmann, 1993; Waddell, Okada & Hasegawa, 1999). In particular, contrasting opinions concerning the names, taxonomic boundaries, number and evolutionary relationships of these species have led to numerous inconsistencies between taxonomic studies. For convenience, we therefore used the species definitions recognized by Hoffmann (1993). Although *Prolagus sardus* was listed in Hoffmann (1993) and included in our supertree, little ecological information is known for this extinct species and thus we excluded it from our analyses.

DATA COLLECTION

Information concerning the coloration and behavioural ecology of each species was principally gleaned from descriptions in Bell, Oliver & Ghose (1990), Chapman & Ceballos (1990), Dobler & Dixon (1990), Duthie & Robinson (1990), Fa & Bell (1990), Flux (1990), Flux & Angermann (1990), Gibb (1990), Smith *et al.* (1990) and Sugimura (1990). These data were supplemented with additional descriptions and photographs in *Grzimek's Animal Life Encyclopedia* (Grzimek, 1990), *Mammalian Species* (American Society of Mammalogists, 1969-present)*,* and *Walker's Mammals of the World* (Nowak, 1999). Data on each of the variables described below were coded in binary format (see Appendix). A value of '1' was assigned to species demonstrating a given variable, a '0' to species that did not display the variable, and a '?' for species for which little or no information on the variable was available.

COLORATION VARIABLES

The basic body coloration of most lagomorphs consists of an overall grey or brownish body hue that lightens ventrally. Our first coloration variable, overall body colour, refers to descriptions of each species' 'upper parts', 'dorsum', 'sides', or 'rump', which are usually the same colour in each species. We examined this variable in terms of the categories grey, red, pale and/or dark based on how species have been described in the literature. Species were scored as dark if they had been described as having a pelage

that included 'black', 'blackish', 'dark brown' or any colour mixed with black, and were labelled as '1' in the dark column in the Appendix. Species displaying other colours (besides those classified as dark) were given a value of '0' in the dark column, while those with no information available on coloration were assigned a value of '?'. This process was repeated for pale, grey and red coloration. Pale body colour included 'white', 'sandy', 'light brown', 'pale grey', 'light grey', 'buffy grey' or 'light buff'. Grey colour referred to 'grey' or 'greyish' coloration. Red colour included 'red', 'rusty', 'chestnut', 'tawny', 'rufous', 'ochraceous', 'cinnamon' or 'auburn' tones. These categories are not mutually exclusive: species with intraspecific variation in coloration might show several of these overall body colorations and were therefore assigned to more than one category. We also noted whether each species moulted into a white pelage in winter as a separate category.

We examined the ventral coloration of each species by noting pelage descriptions of the 'underparts', 'ventrum', 'belly' or 'abdomen' of each species. The only category was white, which included the descriptions 'white', 'dingy-white', 'whitish', or 'tinged with white'. All other colours were assigned a value of '0'.

Coloration of ear tips was divided into dark ('black', 'dark brown', or as 'darker than the other portions of the ear') and white ('white' or 'lighter than the rest of the ear'). Several species fell into neither category (and therefore received values of '0' in both columns), as they displayed ear tip coloration that was the same as that of other portions of the ear. Conversely, species with ear tips changing from black to white seasonally were coded as having both dark and white ear tips.

Finally, we recorded the coloration of tails as dark ('black' or 'dark brown') or white ('white' or 'whitish') if the indicated colours were found on either the dorsal or ventral surface. This variable was not applicable for pikas (*Ochotona* spp.) and the volcano rabbit (*Romerolagus diazi*) as both genera lack visible tails.

ECOLOGICAL VARIABLES

Using descriptions of habitat preferences, we recorded whether each species was typically found in any of the following habitat categories: forests ('alpine', 'tropical', 'boreal', 'deciduous', 'mixed', or 'timberland') and woodlands ('woodland'), scrublands ('scrub', 'bushland', 'riparian', 'riverine', or 'shrub vegetation') and grasslands ('prairie', 'savannah', 'meadows', or 'steppe grasses'), rocky areas ('talus', 'boulders', 'rocky outcrops' or 'crevices'), swamps ('swamp', 'marsh', 'bogland', or 'moorland'), deserts ('desert' or 'arid regions'), tundra ('tundra'), and barren habitats ('bar-

ren land', 'sparse vegetation' or 'no vegetation'). In addition, we noted species that occupied any type of closed (forests, woodlands and swamps) or open (desert, tundra and barren land) habitat.

The continuous variables of altitude or latitude at which species were found were coded in a discrete format so we could include them in our analyses. Records of the highest altitude at which each species was found were ranked across species. To be conservative, we defined only those species in the highest interquartile range as living at high altitude. Using range maps in Chapman & Flux (1990a), we estimated the northern and southern extremes of each species' range. We then noted (by assigning values of '1' for present, or '0' for absent) whether the range of each species fell within either the arctic (80–90 degrees) and subarctic (60–80 degrees) latitude category and/or the tropics (0–10 degrees) and subtropics (10–30 degrees) latitude category.

Finally, we categorized species according to aspects of their behaviour: diurnal activity, nocturnal and/or crepuscular activity, using burrows (known to dig burrows or enter burrows of other species) and social (typically found in pairs, families or colonies, or known to aggregate in groups).

ANALYSES

We derived a small number of predictions for classic coloration hypotheses that have been in the literature for many years (see Ortolani & Caro, 1996). These hypotheses relate to background matching, seasonal variation in pelage colour, countershading, communication and physiology (Table 1). We tested predictions using Fisher exact probability tests as a preliminary examination of the data, and then later using concentrated-changes tests (Maddison, 1990; Maddison & Maddison, 1992) to control for potential phylogenetic effects.

NON-PARAMETRIC TESTS

For each of our Fisher tests, we only included species for which we had information on both the coloration variable of interest and the relevant ecological variable. Thus, the total number of species used varied between analyses. In these non-parametric tests we matched the presence or absence of a coloration trait (the dependent variable) against the presence or absence of an ecological trait (the independent variable; Ortolani & Caro, 1996). Thus, the null hypothesis in each of these tests proposed that the coloration variable was not associated with a particular ecological trait. We examined significance values <0.1 because we were searching for associations using very coarse behavioural and ecological measures.

Table 1. Summary of hypotheses and predictions

Hypotheses	Predictions
Background matching minimizes differences between the animals' coloration and its surroundings.	1. Dark overall body coloration will be associated with closed habitats (forests/woodlands/swamps) 2. Pale overall body coloration will be associated with open, light habitats (desert/tundra/barren land) 3. Grey overall body coloration will be associated with rocky habitats 4. Red overall body coloration will be associated with rocky habitats
Seasonal dimorphism, specifically moulting into a white pelage, is related to conditions associated with snowfall.	5. Species that moult into a white pelage will be associated with arctic/subarctic regions 6. Species that moult into a white pelage will be associated with tundra habitats 7. Species that moult into a white pelage will be associated with high altitudes
Countershading, or pelage coloration that lightens ventrally, minimizes shadows cast upon an animal's lower body.	8. White ventral coloration will be associated with open habitats (desert/tundra/barren land) 9. White ventral coloration will be associated with semi-open habitats (grassland/scrubland) 10. White ventral coloration will be associated with diurnal activity pattern
Ear tips serve a communication function.	11. Dark ear tips will be associated with open habitats (desert/tundra/barren land) in which they would be most conspicuous 12. Dark ear tips will be associated with semi-open habitat types (grassland/scrubland) 13. White ear tips will be associated with dark habitats (forest/woodlands/swamp) in which they would be most conspicuous 14. White ear tips will be associated with semi-open habitat types (grassland/scrubland) 15. Dark ear tips will be associated with diurnal activity (in which these markings might be most conspicuous) 16. White ear tips will be associated with nocturnality and crepuscularity (in which these markings might be most conspicuous) 17. Dark (and white) ear tips will be associated with social species if they serve an intraspecific communication function
Conspicuous tails serve a communication function	18. Dark tails will be associated with open habitats (desert/tundra/barren land) in which they would be most conspicuous 19. Dark tails will be associated with semi-open habitat types (grassland/scrubland) 20. White tails will be associated with dark habitats (forest/woodlands/swamp) in which they would be most conspicuous 21. White tails will be associated with semi-open habitat types (grassland/scrubland) 22. Dark tails will be associated with diurnal activity (in which these markings might be most conspicuous) 23. White tails will be associated with nocturnality and crepuscularity (in which these markings might be most conspicuous) 24. Dark (and white) tails will be associated with social species if they serve an intraspecific communication function
Dark ear tips and dark tails are associated with low temperature	25. Dark ear tips will be associated with the higher regions (arctic/subarctic) 26. Dark ear tips will be associated with species occupying high altitudes 27. Dark tails will be associated with the higher regions (arctic/subarctic) 28. Dark tails will be associated with species occupying high altitudes
Gloger's rule	29. Dark pelages will be found in warm, moist environments (tropical/subtropical regions)

SUPERTREE CONSTRUCTION

While simple non-parametric tests ('cross-species analyses') have been used to identify associations between variables in the past, these tests fail to account for the fact that species values are non-independent: shared character states may reflect common ancestry rather than independent adaptations (Harvey & Pagel, 1991). No robust, well-resolved phylogeny for all extant lagomorph species currently exists to allow for phylogenetic correction, however. Therefore, we constructed a consensus phylogeny of systematic studies in the literature over the last century using the method of supertree construction (*sensu* Sanderson *et al.*, 1998). By combining phylogenetic trees rather than the primary data, supertree construction allows the combination of otherwise incompatible data types (see Bininda-Emonds, Gittleman & Purvis, 1999). Thus, more data types can be used, in keeping with the principle of total evidence (*sensu* Kluge, 1989). Moreover, recent simulation studies show supertree construction to be at least as robust as traditional phylogenetic analyses in which the raw data are combined (Bininda-Emonds & Sanderson, 2001).

We identified systematic studies of lagomorphs initially through on-line searches of the Science Citation Index (via the Web of Science), Zoological Record, and the University of California Library system (Melvyl). The paucity of systematic information on lagomorphs meant that it was necessary to collect studies published from 1900 to present (see legend of Fig. 1 for sources). In total, 146 studies were used.

Care was taken to minimize potential non-independence among source studies from the re-use of part or all the data from previously published studies (see Springer & de Jong, 2001). Guidelines for doing so matched those in previously published supertrees (e.g. Purvis, 1995; Bininda-Emonds *et al.*, 1999; Liu *et al.*, 2001; Jones *et al.*, 2002). For clear instances of data duplication (e.g. same data source or a series of papers by the same authors), we used only the most recent and complete study. Unfortunately, it was often difficult to determine the degree of data duplication because the majority of systematic studies of lagomorphs do not make reference to an explicit data set. Some non-independence is inevitable when source trees rather than the primary data are combined. However, the use of different combinations of data sets, methods of analysis, and assumptions between studies means that different phylogenetic estimates can arise even when non-independence on the level of the data is high (Bininda-Emonds, Gittleman & Steel, 2002). Therefore, we feel that any deleterious effects arising from data duplication are minimal.

The topologies of the source trees were encoded and combined using the supertree method matrix representation with parsimony (MRP) (Baum, 1992; Ragan, 1992). In MRP, nodes in each source tree are encoded in turn. Species descended from a given node are scored as '1', otherwise '0' unless they are missing from that particular source tree entirely in which case they receive '?'. When a study included multiple, non-independent statements of phylogeny (e.g. multiple equally most-parsimonious solutions), only each unique clade from the set of trees was included (see Bininda-Emonds & Bryant, 1998). The matrix representations of each source tree are then combined in a single matrix which includes a hypothetical outgroup comprised completely of zeros to polarize the elements (e.g. root the supertree). This matrix is then analysed using maximum parsimony to infer the supertree.

We used PAUP* v.4.0b4 (Swofford, 1999) to perform parsimony analyses. Because of the large number of taxa (80), we employed a heuristic search strategy consisting of a random addition sequence (1000 replications), TBR branch swapping on minimal trees only, collapsed zero length branches, and unlimited MAXTREES (within memory limitations). Multiple equally parsimonious solutions were summarized as a strict consensus tree, which was taken to be the supertree. Support for the relationships on the supertree was determined using the Bremer decay index (Bremer, 1988; Källersjö *et al.*, 1992).

In the initial parsimony analysis, all characters were weighted equally. However, many of the source trees, particularly from the earlier studies, were derived from taxonomies, species redefinitions, or simple statements of relatedness. Although we feel that such studies contain at least some systematic information, we recognize that this information may not be as robust as that derived from studies employing more rigorous methods (e.g. maximum parsimony or maximum likelihood). Furthermore, the large number of these studies meant that they contributed more elements to the combined matrix (491 vs. 175, or 2.81 times as many), thereby having a potentially greater influence on the topology of the supertree. Yet because these studies are still necessary to infer the supertree (the more robust studies do not examine every species), we weighted elements for the more robust studies (following the guidelines in Purvis, 1995) by a factor of 2.81 so that the two sets of studies had equal input into the supertree. The heuristic search strategy was identical to that described above.

PHYLOGENETIC COMPARISONS

To control for the potential effects of phylogeny, we analysed the same hypotheses as in the non-paramet-

ric tests using Maddison's concentrated-changes test (Maddison, 1990) as implemented in MacClade (Maddison & Maddison, 1992). While other approaches to comparative analyses take into consideration phylogeny branch lengths (e.g. maximum likelihood methodology, Pagel, 1994), this information is very limited for the Order Lagomorpha. Thus, we used concentrated-changes tests, which are based on the topology of a fully resolved phylogeny. We based all analyses on the weighted supertree (see Fig. 2 and description in results section) which contains a polytomy within the genus *Sylvilagus*. The methodology described below was repeated for each of the five equally most-parsimonious resolutions of this polytomy.

Using the matrix depicting each species' character states ('1', '0', or '?'; see Appendix), we mapped the coloration (dependent) and ecological (independent) variables onto the supertree. From the distribution of character states across all species, MacClade reconstructs the evolutionary history of a given trait throughout the tree using parsimony. This makes it possible to count the number of evolutionary gains (change in a character state from a '0' to a '1') and losses (change from a '1' to a '0') in either the coloration or ecological variables (see Maddison & Maddison,

1992). In those instances where character reconstruction was ambiguous (i.e. the supertree contained areas where both '0' or '1' are equally parsimonious), we used 'equivocal cycling' within MacClade to generate all possible reconstructions of the character. When states were equivocal, we chose to examine 'all most-parsimonious states' at each node. Because multiple ambiguities for the same character can lead to many possible reconstructions, we followed the methodology of Ortolani & Caro (1996; see also Ortolani, 1999), and selected the 'most supportive' and the 'least supportive' reconstructions (the reconstructions with the maximum or minimum number of gains or losses, respectively) for further analysis. The most supportive and least supportive reconstructions are equivalent to the first and last reconstructions, respectively, produced by equivocal cycling (Ortolani & Caro, 1996; Ortolani, 1999).

Concentrated-change tests were used to test the probability that as many or more gains and as many or fewer losses in each coloration trait were associated with the presence of a given ecological variable than could be expected by chance. Thus, we examined whether the ecological variable might facilitate either the evolution of the coloration trait (i.e. gains in the

Figure 1. Unweighted supertree of lagomorph relationships in which elements were weighted equally regardless of the robustness of the source study they were derived from. The supertree is a strict consensus of 36 800 equally most-parsimonious solutions (length = 974, CI = 0.684, RI = 0.896, RC = 0.613; the expected CI for 80 taxa is 0.516, Sanderson & Donoghue, 1989). Numbers above branches represent Bremer decay values for that node. In the following list of sources, studies with an asterisk were considered to employ a 'robust' methodology following the guidelines of Purvis (1995) and were used to produce a supertree of higher resolution (see Fig. 2): Abe (1931), Agrawal & Chakraborty (1971), Allen (1927, 1938a,b, 1939), Anderson (1974), Anderson & Gaunt (1962), Angelici & Corti (1990), Angermann (1972; 1983, 1992 [cited as 'in litt.' in Hoffmann, 1993]), Ansell (1978), Argyropulo (1948), Averianov (1994a, 1994b*, 1998*, 1999*), Azzaroli-Puccetti (1987), Baker *et al*. (1983), Banfield (1974), Bee & Hall (1956), Biju-Duval *et al*. (1991), Bobrinskii, Kuznetsov & Kuzyakin (1965), Bonhote (1904), Broadbooks (1965), Cai & Feng (1982), Cervantes & Lorenzo (1997), Cervantes *et al*. (1999), Chapman & Ceballos (1990), Chapman *et al*. (1983), Chapman & Flux (1990b), Corbet (1978, 1983, 1984), Corbet & Hill (1991), Dawson (1967), Dice (1929), Diersing (1981a,b), Diersing & Wilson (1980), Dixon *et al*. (1983), Ellerman & Morrison-Scott (1951, 1953, 1966), Erbajeva (1994, 1988), Feng, Cai & Zheng (1986), Feng & Kao (1974), Feng & Zheng (1985), Flux & Angermann (1990), Formozov, Lisovskii & Baklushinskaya (1999), Gonzalez-Cozatl (unpubl.), Goodwin (1946), Grillitsch *et al*. (1992), Gromov & Baranova (1981), Gureev (1964), Halanych *et al*. (1999*), Halanych & Robinson (1997*, 1999*), Hall (1951, 1981), Heptner (1934), Hershkovitz (1950), Hibbard (1963), Hilzheimer (1908), Hoffmann (1993), Honacki, Kinman & Koeppl (1982), Howell (1929), Kao & Feng (1964), Koenigswald (1996), Kowalski & Rzebik-Kowalska (1991), Lorenzo (1987), Lundholm (1955), Lydekker (1907), Lyon (1904), Ma (1986), Meester *et al*. (1986), Miller (1912a,b), Miller & Kellog (1955), Miller & Rehn (1901), Mitchell (1978), Monnerot *et al*. (1994*), Nelson (1907, 1909), Ognev (1929, 1940), Orr (1940), Osgood (1932), Palacios (1979, 1996), Pavlinov *et al*. (1995), Pavlinov & Rossolimo (1987), Peddie (1975), Pérez-Suárez, Palacios & Boursot (1994*), Petter (1959, 1961, 1963, 1972), Pierpaoli *et al*. (1999*), Pringle (1974), Pucek (1981), Rausch (1953, 1963), Rautenbach (1982), Rekovets (1990), Roberts (1951, 1977), Robinson (1982), Robinson & Dippenaar (1983a,b), Robinson, Elder & Chapman (1983), Robinson & Osterhoff (1983), Robinson *et al*. (1984), Ruedas (1998*), Saint-Girons (1973), Samoil & Samuel (1981), Schneider & Leipoldt (1983), Shortridge (1934), Simpson (1945), Smith *et al*. (1990), Smithers (1971, 1990), Smorkatsheva, Aristov & Aksenova (1990), St. Leger (1929), Swanepoel, Smithers & Rautenbach, 1980), Tate (1947), Thenius (1969), Thomas (1903, 1922), Thomas & Hinton (1923), Tomida (1997), Toschi (1965), Vinogradov & Argyropulo (1941), Vinogradov & Gromov (1952), Vorontsov & Ivanitskaya (1973), Weston (1981, 1982*), White (1991), Yom-Tov (1967), Youngman (1965), Yu, Zneng & Feng (1992*), Yu, Zheng & Shi (1997*), Yu *et al*. (2000*), and Zhou & Xia (1981).
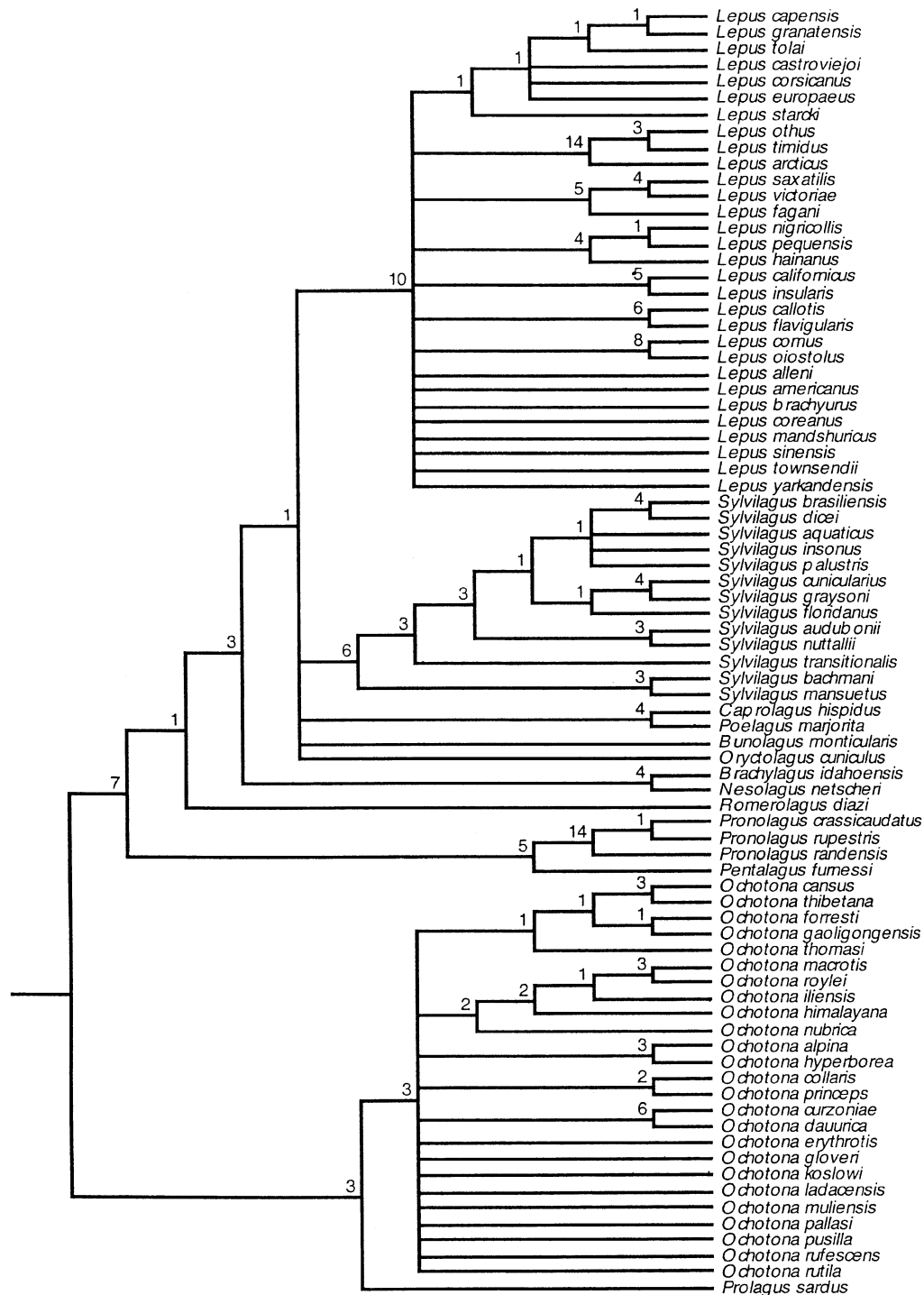
coloration trait were associated with the ecological variable) and/or the maintenance of the coloration trait (i.e. losses of the coloration trait were not associated with the ecological variable). The null hypothesis, tested against a distribution derived through simulation and 10 000 replicates, was that gains and losses in a given coloration variable were randomly distributed on the tree with respect to the ecological variable. When ambiguity in character reconstruction existed – multiple reconstructions resulted in two or four probability values, depending on whether one or both of the dependent and independent variables
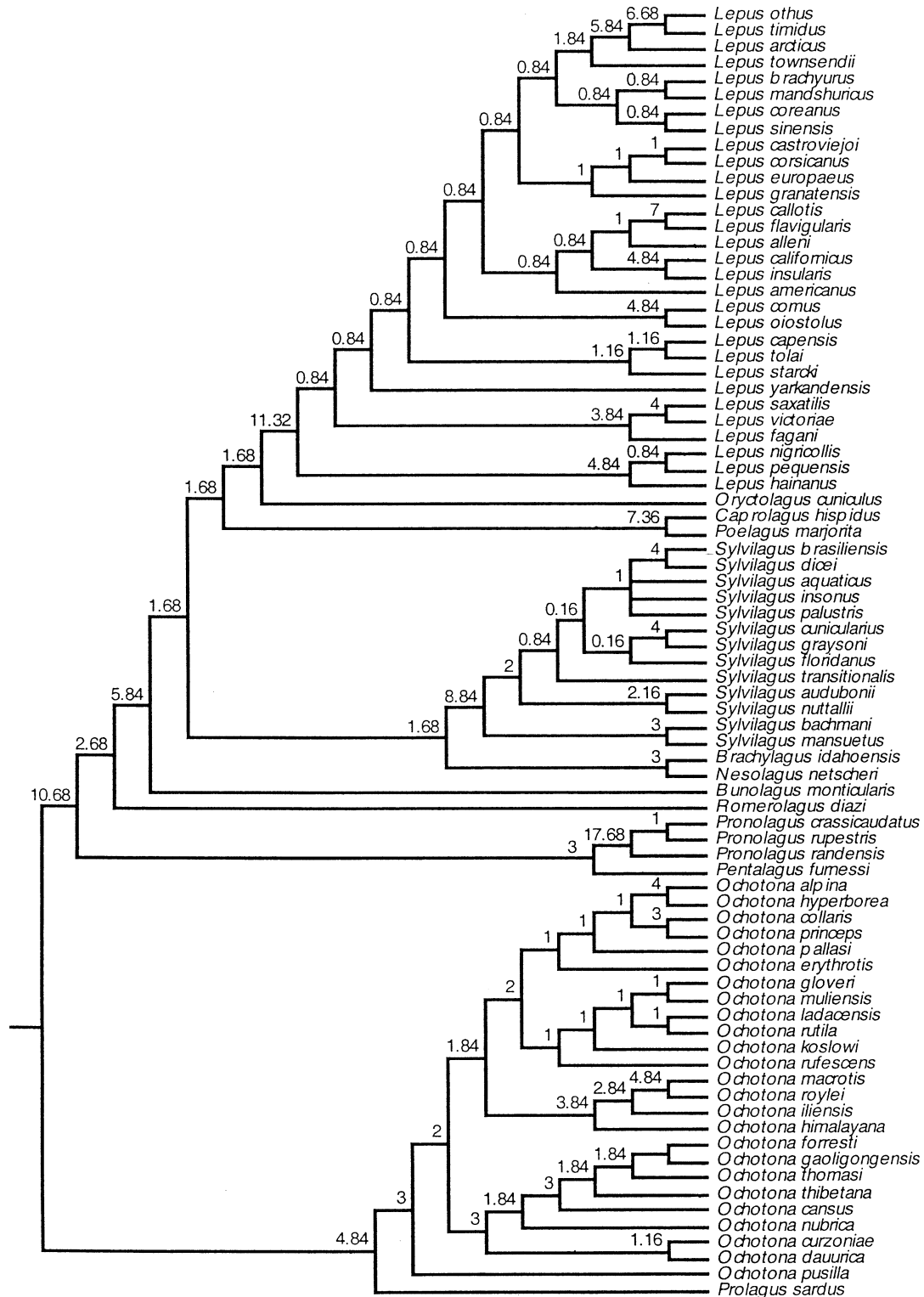
Figure 2. Weighted supertree of lagomorph relationships in which elements derived from more robust studies were weighted by a factor of 2.84 to have an equal influence on the supertree as elements derived from less robust studies. The supertree is a strict consensus of five equally most-parsimonious solutions (length = 1460.79, CI = 0.673, RI = 0.888, RC = 0.597). Numbers above branches represent Bremer decay values for that node. See legend of Figure 1 for studies included in the lagomorph supertree (studies with an asterisk were weighted).

displayed ambiguity – we examined significant values <0.1 and applied Bonferroni corrections to these tests. Thus, if four tests had been conducted, we considered an association significant if $P < 0.025$ (i.e. 0.1/4). Only the most significant P-value is reported in the text.

RESULTS

A SUPERTREE OF LAGOMORPHA

Supertree construction in which all elements were weighted equally regardless of the inferred robustness of the source study yielded 36 800 equally most-parsimonious trees (MPTs), each of 974 steps. This many MPTs increases the likelihood of searches stalling on less than optimal solutions or of not finding all equally parsimonious solutions. However, we are reasonably confident that we avoided both pitfalls due to the large number of random addition sequences used, and based on subsequent analyses using the parsimony ratchet (Nixon, 1999) and a compartmentalization approach (Mishler, 1994). Understandably, the high number of MPTs meant that the supertree was poorly resolved (only 73.4% with respect to a fully bifurcating tree), especially within the genera *Lepus* and *Ochotona* (Fig. 1). Although various goodness-of-fit statistics are high, we infer that lack of resolution is generally due to conflict between the source trees rather than a lack of information. As measured by the Bremer decay index, support for the inferred relationships were generally low throughout the tree. Most genera showed higher levels of support, as did a few species pairs within *Lepus*, *Ochotona* and *Sylvilagus*.

In contrast, a much more resolved supertree resulted from weighting source trees to favour those based on more robust methodologies. Only five MPTs were found, each of 1460.79 steps, and the supertree is 97.5% resolved (Fig. 2). This weighted supertree is not a more resolved version of the unweighted one. The positions of *Ochotona cansus*, *Ochotona thibetana*, *Bunolagus*, the clade of *Brachylagus* plus *Nesolagus*, and several clades within *Lepus* are inconsistent between the two trees. Despite being more resolved than the unweighted supertree, Bremer support values remained low for most clades on the weighted supertree. In fact, the support values were proportionately lower than for the unweighted supertree on average, indicating that the conflict between source studies remains and that the additional resolution should be treated cautiously. Goodness-of-fit statistics also displayed slightly lower values than those of the unweighted supertree. Despite this, we feel that the weighted tree is superior because of the greater weight it gives to studies employing more robust methodologies and we therefore used this tree for the concentrated-changes analyses.

ANALYSES

Background matching
Using a Fisher exact probability test, dark coloration was marginally significantly associated with species that occupy forest or woodland habitats ($N = 76$, $P = 0.095$) but not in a concentrated-changes test controlling for phylogeny. Pale overall coloration was significantly associated with desert, tundra and barren land habitats (Fisher: $N = 76$, $P = 0.001$) and desert habitats alone (Fisher: $N = 76$, $P = 0.003$) and these associations were strongly supported after controlling for phylogeny ($P = 0.02$, $P = 0.008$, respectively). Grey coloration was only associated with rocky habitats in Fisher exact probability tests ($N = 76$, $P = 0.098$) but not after controlling for phylogeny. Red coloration was not significantly associated with rocky habitats in the non-parametric tests, but was associated with these habitats in concentrated-changes tests ($P = 0.03$).

Seasonal variation
In non-parametric tests, white winter pelage was strongly associated with arctic and subarctic regions combined ($N = 75$, $P = 0.001$), as well as with tundra habitat ($N = 75$, $P = 0.003$). After controlling for the shared ancestry, however, these results disappeared.

Countershading
Species displaying white ventral surfaces were marginally associated with diurnal activity (Fisher: $N = 48$, $P = 0.059$) but not with open (deserts, tundra and barren land) habitats. White ventral surfaces were associated with grassland and scrubland habitats in one concentrated-changes test ($P = 0.058$), but this result depended heavily on the character reconstruction.

Ear tips and communication
Fisher tests revealed that dark ear tips were significantly associated with species that do not demonstrate diurnal activity ($N = 64$, $P < 0.001$) but were not associated with open habitats, semi-open habitats (grassland and scrubland), or sociality. In concentrated-changes tests however, dark ear tips were significantly associated with sociality (in one reconstruction, $P = 0.09$).

Using a Fisher test, white ear tips were significantly associated with species that did not inhabit closed habitats ($N = 70$, $P = 0.023$), but this result

was lost using a concentrated-changes test. White ear tips were not significantly associated with grassland and scrubland habitats, nocturnal and crepuscular activity patterns or sociality in either set of tests.

Tails and communication

Fisher tests revealed a significant association between tails displaying black or dark brown coloration and species that do not use burrows ($N = 41$, $P = 0.003$). In concentrated-changes tests dark tails were not associated with any ecological variables following Bonferroni corrections. Tails displaying white coloration showed no significant associations with closed (forest, woodland and swamp) habitats, semi-open habitats, or burrow use in Fisher exact probability tests, but there was a marginal association with sociality ($N = 37$, $P = 0.092$). After controlling for phylogeny, white tails were significantly associated with grassland and scrubland habitats ($P = 0.0182$), sociality ($P = 0.024$), and burrow use ($P = 0.06$). Since all the leporid species for which we had data demonstrated some nocturnal or crepuscular activity (although some were also diurnal) we could not test for an association between tail colour and activity pattern.

Dark coloration on extremities in relation to cold environments

Fisher and concentrated-changes tests indicated that dark ear tips were not significantly associated with arctic and subarctic regions or with high altitudes. However, dark tails were associated with these two variables using Fisher tests ($N = 51$, $P = 0.057$; $N = 41$, $P = 0.001$, respectively).

Coloration and latitude

Fisher tests provided weak support for Gloger's rule, that darker pelage coloration is more likely in humid environments: dark overall coloration was associated with tropic and subtropic latitudes ($N = 77$, $P = 0.062$). This association, however, was not supported in concentrated-changes tests.

DISCUSSION

Lagomorph phylogeny

The supertree analyses confirm the historical uncertainty over lagomorph systematics (see also Hoffmann, 1993). Both the poor resolution of the unweighted supertree and the low Bremer decay values in both trees (unweighted and weighted) reveal a general lack of consensus among the source studies. At best, only the various genera and a few species pairs within them showed reasonable amounts of support. It is likely that the support for these genera is somewhat

inflated as well: studies of higher taxonomic levels often tacitly assume the monophyly of the genera. Despite attempting to identify and include only those species analysed in each phylogenetic study, we were often forced to include all members of a genus, thereby overwhelming those few studies that advocate the paraphyly of some genera (e.g. *Lepus* in Averianov, 1998).

The uncertainty surrounding lagomorph systematics derives from several causes. First, species definitions and synonymies are still disputed in many cases (see Chapman & Flux, 1990b; Hoffmann, 1993). Second, a comprehensive phylogenetic analysis across the order, and one that uses a robust methodology, is lacking. Many of these studies focus on only those species found within a certain geographical region (e.g. South Africa or Russia). In addition, research efforts tend to examine the same selected set of species within major genera (e.g. *Lepus*, *Ochotona* and *Sylvilagus*). Very few studies, most of them based on morphological data, have examined the relationship of monotypic genera such as *Poelagus*, *Pentalagus*, *Romerolagus*, *Nesolagus* and *Caprolagus*. Finally, only 15 of the 146 source studies (10.2%) present results derived from more rigorous methodologies (as defined by Purvis, 1995). Unfortunately, these 15 studies are insufficient in themselves to derive a supertree of all lagomorph species. In short, the Lagomorpha present a difficult systematic problem, especially if morphological data are used. An exhaustive and systematic molecular investigation of all the lagomorphs is desperately needed.

It is therefore difficult to know how to interpret associations between coloration and ecological variables, especially in a phylogenetic context. Although the supertree is generally weakly supported, we feel this is an accurate reflection of the present state of lagomorph systematics and represents the best available estimate of lagomorph phylogeny because it is derived from all available morphological and molecular data ('total evidence', *sensu* Kluge, 1989). Widespread consensus exists that the most robust phylogenetic inferences are those supported by the most independent lines of evidence (Mickevich, 1978; Farris, 1983; Penny & Hendy, 1986; Kluge, 1989; Novacek, 1992; de Jong, 1998). So long as homoplasy is randomly distributed both among features and the relationships it infers (see Sanderson & Hufford, 1996), surveying as many features as possible should reveal the true phylogenetic history of a group.

Background matching

Our research strategy was to examine whether the origin and maintenance of coloration patterns were asso-

ciated with particular ecological variables. In both non-parametric and concentrated-changes tests, we found strong associations between pale overall body coloration and species living in open habitats (deserts, tundra and barren land), particularly deserts. Associations between pale fur colour and deserts have been noted for the antelope jackrabbit (*Lepus alleni*), black-tailed jackrabbit (*Lepus californicus*) and Arizona cottontail (*Sylvilagus audubonii*; Dice & Blossom, 1937) as well as for rodents such as the Apache pocket mouse (*Perognathus apache*; Dice & Blossom, 1937) and the old field mouse (*Peromyscus polionotus*; Osgood, 1909; Belk & Smith, 1996), and more generally across the Canidae (Ortolani & Caro, 1996). Our analyses do not address whether pale coloration is an adaptation for concealment or thermoregulation, but two arguments speak to the former. An association was found between pale coloration and habitats that included tundra and barren land. Pale coloration might be expected to be less conspicuous in habitats that are frequently covered in snow (tundra) or devoid of dark vegetation (barren land), but less important for reducing heat absorption in these cold environments. There is also experimental evidence to show that both aerial (Dice, 1947; Kaufman, 1974) and terrestrial (Brown, 1965) predators select against conspicuously coloured mice.

Associations have also been found between dark fur and dark soil, as for example in pocket gophers (*Thomomys bottae*; Goldman, 1935), deer mice (*Peromyscus maniculatus*; Dice & Blossom, 1937), grasshopper mice (*Onchomys leucogaster*; Merriam, 1890) and white-throated woodrats (*Neotoma albigula*; Benson, 1936). Here, we could muster only weak support using Fisher exact probability tests that lagomorphs demonstrate an association between dark environments, such as forests, and the evolution of dark pelage coloration. There was some evidence that both grey and red coloration are associated with rocky habitats, particularly in the latter case.

SEASONAL VARIATION

Cott (1940) remarked that some arctic hares (*Lepus arcticus*) remain white all year round; the varying hare (*Lepus americanus*) turns white in winter; whilst some hares ranging farther south retain their summer coat all year round. We confirmed these observations by showing that white winter pelage was strongly associated with both arctic and subarctic regions and with tundra habitat. A similar result has been found across carnivores, in general, and canids and mustelids in particular (Ortolani & Caro, 1996). In lagomorphs, however, this association appears to derive largely from shared ancestry. Most of the arctic and subarctic species displaying white winter pelage form a single clade (from *Lepus townsendii + L. arcticus + L. timidus + L. othus*) such that the null hypothesis could not be rejected in concentrated-changes tests.

COUNTERSHADING

Our analyses revealed an association between white ventral surfaces and diurnal activity, but not between white underparts and any particular habitat type. Indeed, nearly all lagomorphs have light ventral surfaces, suggesting perhaps that this trait minimizes shadow in most habitats. Nevertheless, there are other explanations for countershading such as dorsal pigmentation shielding against ultraviolet radiation that were not tested here.

EAR TIPS AND COMMUNICATION

Lagomorphs with dark ear tips were unlikely to be diurnal based on Fisher tests, but this association was not supported after taking shared ancestry into account. Dark ear tips were associated with social species after controlling for phylogeny. Species with white ear tips were less likely to live in closed habitats (forests, woodlands and swamps), but this also seemed to be a case of phylogenetic inertia. The fact that dark ear tips were not associated with cold regions or high altitudes argues against the idea that such coloration results from melanocyte production in colder parts of the body. Instead, the results taken together suggest a communication function associated with being social, implicating intraspecific signalling. A signalling hypothesis is reinforced by similar findings in carnivores, where felids with black ear tips were more likely to live in grasslands (depending on the phylogenetic reconstruction), and that carnivores in general, and felids in particular, were more likely to live in forested habitats (Ortolani & Caro, 1996). Ear markings in both carnivores and lagomorphs might allow conspecifics to follow each other through vegetation (Schaller, 1967; Leyhausen, 1979), which would help explain the possible association with sociality in lagomorphs (under a concentrated-changes test); they could reinforce displays during intraspecific competition (Fox, 1971); or act as signals between prey and predators (Holley, 1993) although this explanation is less likely to apply to carnivores. At present we cannot distinguish between these hypotheses.

TAILS AND COMMUNICATION

There were few associations between dark tails and ecological or behavioural variables. Fisher and

concentrated-changes tests (some reconstructions) revealed that species with white tails tended to be social. White tails were also associated with grassland and scrubland habitats and burrow use when using some character reconstructions. The former results suggest that light-coloured tails are used in intraspecific communication. Perhaps the vivid white ventral surface that is exposed by lifting the tail during flight may provide a signal to conspecifics. These results stand in contrast to findings from carnivore families where it was found that possession of a conspicuous tail tip was not associated with sociality (Ortolani & Caro, 1996).

COLORATION AND TEMPERATURE

Dark tails were associated with cold climates using cross-species comparisons but not after controlling for phylogeny. These results lend partial support to claims that dark extremities result from differential melanocyte production in colder areas on the body, although they are contradicted by the findings from dark ears.

Gloger's rule was originally formulated from empirical observations that dark coats were more prevalent in humid habitats but the adaptive basis for this was never made explicit. In lagomorphs, there was a significant association between dark overall coloration and living in tropical and subtropical latitudes (areas that are likely to be humid) in Fisher tests. This result might be credited to shared ancestry, however, as concentrated-changes tests yielded little support for Gloger's rule. Thus lagomorphs stand in contrast to carnivores where dark coats are more prevalent in tropical forests (Ortolani & Caro, 1996).

CONCLUSIONS

Our study represents the first attempt to apply a rigorous methodology to explain the adaptive significance of pelage coloration in lagomorphs. Both nonparametric tests and comparisons that accounted for possible similarity due to common ancestry indicated significant associations between pale coloration and open habitats, particularly deserts, and between white tails and sociality. The latter tests also indicated associations between red coloration and rocky habitats, dark ear tips and sociality, white coloration on tails and grassland and scrubland habitats, and white coloration on tails and burrow use. These findings indicate that camouflage and communication are two important factors influencing coloration in lagomorphs. Our findings lend support to the hypotheses that

overall body coloration evolves to match the animal's background, and that extremities act as conspicuous signals to conspecifics and perhaps to predators. Our analyses did not support the hypotheses that white ventral surfaces aid in concealment or extremities are dark due to exposure to cold temperatures. It is hoped that our findings will spur more interest in this little-studied group of mammals, both in terms of ecological and phylogenetic research.

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REFERENCES

Abe Y. 1931. A synopsis of the Leporine Mammals of Japan. *Journal of Science of the Hiroshima University, Series B, Zoology* **1:** 45–63.

Agrawal VC, Chakraborty S. 1971. Notes on a collection of small mammals from Nepal, with the description of a new mouse-hare (Lagomorpha: Ochotonidae). *Proceedings of the Zoological Society, Calcutta* **24:** 41–46.

Allen GM. 1927. Lagomorphs collected by the Asiatic Expeditions. *American Museum Novitates* **284:** 1–11.

Allen GM. 1938a. Zoological results of the second Dolan Expedition to western China and eastern Tibet, 1934–36. Part III. Mammals. *Proceedings of the Academy of Natural Sciences of Philadelphia* **90:** 269–270.

Allen GM. 1938b. The mammals of China and Mongolia. *American Museum of Natural History* **11:** 1–620.

Allen GM. 1939. A checklist of African mammals. *Bulletin of the Museum of Comparative Zoology* **83:** 1–763.

American Society of Mammalogists 1969-present. *Mammalian species*. New York: American Society of Mammalogists.

Anderson HL. 1974. Natural history and systematics of the tundra hare (*Lepus othus* Merriam) in western Alaska. Unpublished MSc Thesis. Fairbanks: University of Alaska.

Anderson S, Gaunt AS. 1962. *A classification of the white-sided jack rabbits of Mexico. American Museum Novitates, no. 2088.* New York: American Museum of Natural History.

Angelici FM, Corti M. 1990. Systematics and geographic variation of the pikas (Lagomorpha: Ochotonidae) in the Palaearctic Region. I. Preliminary results on *Ochotona rufescens*, *O. roylei*, *O. thibetana* and *O. cansus*. *Atti della Accademia Nazionale dei Lincei Classe di Scienze Fische Mathematiche e Naturali Rendiconti Lencei Scienze Fisiche e Naturali* **1:** 171–176.

Angermann R. 1972. Hares, rabbits and pikas. In: Grzimek B, ed. *Grzimek's animal life encyclopedia*, Vol. 12. New York: Van Nostrand Reinhold Co, 419–462.

Angermann R. 1983. The taxonomy of Old World *Lepus*. *Acta Zoologica Fennica* **174:** 17–21.

Angermann R, Flux JEC, Chapman JA, Smith AT. 1990. Lagomorph classification. In: Chapman JA, Flux JEC, eds. *Rabbits, hares and pikas: status conservation action plan*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 7–13.

Ansell WFH. 1978. *The mammals of Zambia*. Chilanga: Department of National Parks and Wildlife Service.

Argyropulo AI. 1948. Obzor retsentnykh vidov cem. [A review of recent species of the family Lagomyidae Lilljeb., 1886 (Lagomorpha, Mammalia)]. *Trudy Zoologicheskovo Insituta, Akademiya Nauk USSR, Leningrad* **7:** 124–128. (In Russian).

Averianov AO. 1994a. Morphotypic variation of the skull and teeth in east-Asian species of the genus *Lepus* (Lagomorpha, Leporidae). *Zoologicheskii Zhurnal* **73:** 132–139. (In Russian).

Averianov AO. 1994b. On the taxonomic position of the genus *Lepus* within the family Leporidae (Mammalia, Lagomorpha). *Zoologicheskii Zhurnal* **73:** 97–107. (In Russian).

Averianov AO. 1998. Subgeneric systematics of hares of the genus *Lepus* (Lagomorpha, Leporidae). *Byulleten' Moskovskogo Obshchestva Ispytatelei Prirody Otdel Biologicheskii* **103:** 3–8. (In Russian).

Averianov AO. 1999. Phylogeny and classification of Leporidae (Mammalia, Lagomorpha). *Vestnik Zoologii* **33:** 41–48.

Azzaroli-Puccetti ML. 1987. The systematic relationships of hares (genus *Lepus*) of the Horn of Africa. *Cimbebasia (A)* **9:** 1–14.

Baker AJ, Eger JL, Peterson RL, Manning TH. 1983. Geographic variation and taxonomy of arctic hares. *Acta Zoologica Fennica* **174:** 45–48.

Banfield AWF. 1974. *The mammals of Canada*. Toronto, Ontario: University of Toronto Press.

Baum BR. 1992. Combining trees as a way of combining data sets for phylogenetic inference, and the desirability of combining gene trees. *Taxon* **41:** 3–10.

Beddard FE. 1892. *Animal coloration: an account of the principal facts and theories related to the colours and markings of animals*. London: Swan and Sonnenschein.

Bee JW, Hall ER. 1956. Mammals of northern Alaska on the arctic slope. *Miscellaneous Publications, Museum of Natural History, University of Kansas Publications* **8:** 1–309.

Belk MC, Smith MH. 1996. Pelage coloration in oldfield mice (*Peromyscus polionotus*): antipredator adaptation? *Journal of Mammalogy* **77:** 882–890.

Bell DJ, Oliver WLR, Ghose RK. 1990. The Hispid Hare *Caprolagus hispidus*. In: Chapman JA, Flux JEC, eds. *Rabbits, hares and pikas: status conservation action plan*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 129–136.

Benson SB. 1936. Concealing coloration among some desert rodents of the southwestern United States. *University of California Publications in Zoology* **40:** 1–69.

Biju-Duval C, Ennafaa H, Dennebouy N, Monnerot M, Mignotee F, Soriguer RC, Gaaïed AE, Hili AE, Mounolou J-C. 1991. Mitochondrial DNA evolution in Lagomorphs: origin of systematic heteroplasmy and organization of diversity in European rabbits. *Journal of Molecular Evolution* **33:** 92–102.

Bininda-Emonds ORP, Bryant HN. 1998. Properties of matrix representation with parsimony analyses. *Systematic Biology* **47:** 497–508.

Bininda-Emonds ORP, Gittleman JL, Purvis A. 1999. Building large trees by combining phylogenentic information: a complete phylogeny of the extant Carnivora (Mammalia). *Biological Reviews (Cambridge)* **74:** 143–175.

Bininda-Emonds ORP, Gittleman JL, Steel MA. 2002. The (super) tree of life: procedures, problems, and prospects. *Annual Review of Ecology and Systematics* **33:** 265–289.

Bininda-Emonds ORP, Sanderson MJ. 2001. An assessment of the accuracy of MRP supertree construction. *Systematic Biology* **50:** 565–579.

Bobrinskii NA, Kuznetsov BA, Kuzyakin AP. 1965. *Opredelitel' mlekopitayushchikh SSSR [Key to the mammals of the USSR.]* Moscow: Sovietskaya Nauka. (In Russian).

Bonhote JL. 1904. On the mouse-hares of the genus *Ochotona*. *Proceedings of the Zoological Society of London* **2:** 205–219.

Bremer K. 1988. The limits of amino acid sequence data in angiosperm phylogenetic reconstruction. *Evolution* **42:** 795–803.

Broadbooks HE. 1965. Ecology and distribution of the pikas of Washington and. Alaska. *American Midland Naturalist* **73:** 299–335.

Brown LN. 1965. Selection in a population of housemice containing mutant individuals. *Journal of Mammalogy* **46:** 461–465.

Cai G, Feng Z. 1982. A systematic revision of the subspecies of highland hare (*Lepus oiostolus*), including 2 new subspecies. *Acta Theriologica Sinica* **2:** 167–182. (In Chinese).

Cervantes FA, Lorenzo C. 1997. Morphometric differentiation of rabbits (*Romerolagus* and *Sylvilagus*) and jackrabbits (*Lepus*) of Mexico. *Gibier Faune Sauvage, Game Wildlife* **14:** 405–425.

Cervantes FA, Ramirez-Silva JP, Marin A, Portales GL. 1999. Allozyme variation of cottontail rabbits (*Sylvilagus*) from Mexico. *Zeitschrift für Säugetierkunde* **64:** 356–362.

Chapman JA, Ceballos G. 1990. The cottontails. In: Chapman JA, Flux JEC eds. *Rabbits, hares and pikas: status conservation action plan*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 95–110.

Chapman JA, Dixon KR, Lopez-Forment W, Wilson DE. 1983. The New World jackrabbits and hares (genus *Lepus*). 1. Taxonomic history and population status. *Acta Zoologica Fennica* **174:** 49–51.

Chapman JA, Flux JEC, eds. 1990a. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources.

Chapman JA, Flux JEC. 1990b. Introduction and overview of the Lagomorphs. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 1–6.

Corbet GB. 1978. *The mammals of the palaearctic region: a taxonomic review.* London: Cornell University Press/British Museum (Natural History).

Corbet GB. 1983. A review of classification in the family Leporidae. *Acta Zoologica Fennica* **174:** 11–15.

Corbet GB. 1984. *The mammals of the palaearctic region: a taxonomic review (Suppl.).* London: British Museum (Natural History).

Corbet GB, Hill JE. 1991. *A world list of mammalian species*, 3rd edn. London: British Museum (Natural History).

Cott HB. 1940. *Adaptive coloration in animals*. London: Metheun.

Dawson MR. 1967. Lagomorph history and stratigraphic record. In: Teichert C, Yochelson EL eds. *Essays in paleontology and stratigraphy. Department of Geology, University of Kansas Special Publication* **2:** 287–316.

Dice LR. 1929. The phylogeny of the Leporidae, with description of a new genus. *Journal of Mammalogy* **10:** 340–344.

Dice LR. 1947. Effectiveness of selection by owls of deermice (*Peromyscus maniculatus*) which contrast in color with their background. *Contributions from the Laboratory of Vertebrate Biology, University of Michigan* **34:** 1–20.

Dice LR, Blossom PM. 1937. *Studies of mammalian ecology in southwestern North America with special attention to colors of desert mammals.* Washington, DC: Carnegie Institution.

Diersing VE. 1981a. Systematic status of *Sylvilagus brasiliensis* and *S. insonus* from North America. *Journal of Mammalogy* **62:** 539–556.

Diersing VE. 1981b. The systematic status of several species of cottontails (genus *Sylvilagus*) from North and South America. In: Myers K, MacInnes CD eds. *Proceedings of the world lagomorph conference*. Guelph, Ontario: Guelph University Press, 98.

Diersing VE, Wilson DE. 1980. Distribution and systematics of the rabbits (*Sylvilagus*) of west-central Mexico. *Smithsonian Contributions to Zoology* **297:** 1–34.

Dixon KR, Chapman JA, Willner GR, Wilson DE, Lopez-Forment W. 1983. The New World jackrabbits and hares (genus *Lepus*). 2. Numerical taxonomic analysis. *Acta Zoologica Fennica* **174:** 53–56.

Dobler FC, Dixon KR. 1990. The pygmy rabbit *Brachylagus idahoensis*. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 111–115.

Duthie AG, Robinson TJ. 1990. The African rabbits. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 121–127.

Ellerman JR, Morrison-Scott TCS. 1951. *Checklist of palaearctic and Indian mammals 1758–1946.* London: British Museum (Natural History).

Ellerman JR, Morrison-Scott TCS. 1953. *South African mammals 1758–1951: a reclassification*. London: British Museum (Natural History).

Ellerman JR, Morrison-Scott TCS. 1966. *Checklist of palaearctic and Indian mammals 1758–1946*, 2nd edn. London: British Museum (Natural History).

Erbajeva MA. 1988. *Pishchukhi kainozoya.* [*Pikas of the Cenozoic age.*] Moscow-Leningrad: 'Nauka'. (In Russian).

Erbajeva MA. 1994. Phylogeny and evolution of Ochotonidae with emphasis on Asian Ochotonids. In: Tomida Y, Li C, Setoguchi T eds. *Recent and lagomorph families of Asian origins and diversification.* Tokyo: National Science Museum Monographs, no. 8, 1–13.

Fa JE, Bell DJ. 1990. The volcano rabbit *Romerolagus diazi*. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 143–146.

Farris JS. 1983. The logical basis of phylogenetic analysis. In: Platnick NI, Funk VA eds. *Advances in cladistics*. New York: Columbia University Press, 7–36.

Feng TC, Kao Y. 1974. Taxonomic notes on the Tibetan pika and allied species—including a new subspecies. *Acta Zoologica Sinica* **20:** 76–87. (In Chinese).

Feng Z, Cai G, Zheng C. 1986. *The mammals of Xizang*. Beijing: Science Press. (In Chinese).

Feng Z, Zheng C. 1985. Studies on the pikas (genus *Ochotona*) of China- taxonomic notes and distribution. *Acta Theriologica Sinica* **5:** 269–290. (In Chinese).

Flux JEC. 1990. The Sumatran rabbit *Nesolagus netsheri*. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 137–139.

Flux JEC, Angermann R. 1990. The hares and jackrabbits. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 61–94.

Formozov NA, Lisovskii AA, Baklushinskaya I Yu. 1999. Karyological diagnostics of pikas (*Ochotona*, Lagomorpha) from the Putorana Plateau (Northern Central Siberia). *Zoologicheskii Zhurnal* **78:** 606–612.

Fox MW. 1971. *Behaviour of wolves, dogs and related canids*. New York: Harper & Row.

Gibb JA. 1990. The European rabbit *Oryctolagus cuniculus*. In: Chapman JA, Flux JEC eds. *Rabbits, hares, and pikas: status survey and conservation action plan.* Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 116–120.

Gloger CWL. 1833. *Das Abandern der Vogel durch Einfluss des Klimas.* [The effect of climatic change on birds]. Breslau: A. Schulz. (In German).

Goldman EA. 1935. Pocket gophers of the *Thomomys bottae* groups in the United States. *Proceedings of the Biological Society of Washington* **48:** 153–158.

Goodwin GG. 1946. Mammals of Costa Rica. *Bulletin of the American Museum of Natural History* **87:** 271–473.

Grillitsch M, Hartl GB, Suchentrunk F, Willing R. 1992. Allozyme evolution and the molecular clock in the Lagomorpha. *Acta Theriologica* **37:** 1–13.

Gromov IM, Baranova GI. 1981. *Katalog mlekopitayuschchikh USSR.* [Catalogue of the mammals of the USSR]. Moscow-Leningrad: Nauka. (In Russian).

Grzimek B. 1990. *Grzimek's animal life encyclopedia.* New York: Van Nostrand Reinhold Co.

Gureev AA. 1964. *Fauna SSSR, mklekopitayushchie, tom. 3, vyp. 10, Zaitseobraznye (Lagomorpha). [Fauna of the USSR, Mammals, vol. 3, part 10, Lagomorpha].* Moscow-Leningrad: Nauka. (In Russian).

Halanych KM, Demboski JR, Van Vuuren BJ, Klein DR, Cook JA. 1999. Cytochrome b phylogeny of North American hares and jackrabbits (*Lepus*, Lagomorpha) and the effects of saturation in outgroup taxa. *Molecular Phylogenetics and Evolution* **11:** 213–221.

Halanych KM, Robinson TJ. 1997. Phylogenetic relationships of cottontails (*Sylvilagus*, Lagomorpha): congruence of 12S rDNA and cytogenetic data. *Molecular Phylogenetics and Evolution* **7:** 294–302.

Halanych KM, Robinson TJ. 1999. Multiple substitutions affect the phylogenetic utility of cytochrome b and 12S rDNA data: Examining a rapid radiation of leporid (Lagomorpha) evolution. *Journal of Molecular Evolution* **48:** 369–379.

Hall ER. 1951. A synopsis of the North American Lagomorpha. *University of Kansas Publications, Museum of Natural History* **5:** 119–202.

Hall ER. 1981. *The mammals of North America*, 2nd edn. New York: John Wiley and Sons.

Harvey PH, Pagel MD. 1991. *The comparative method in evolutionary biology.* Oxford: Oxford University Press.

Heptner WG. 1934. Systematische und tiergeographische Notizen über einige russische Sauger. [Systematic and biogeographical notes on selected Russian mammals]. *Folia Zoologica et Hydrobiologica* **6:** 17–24.

Hershkovitz P. 1950. Mammals of Northern Colombia. Preliminary Report, 6. Rabbits (Leporidae), with notes on the classification and distribution of the South American forms. *Proceedings of the United States National Museum* **100:** 327–375.

Hibbard CW. 1963. The origin of the P3 Pattern of *Sylivilagus*, *Caprolagus*, *Orytolagus*, and *Lepus*. *Journal of Mammalogy* **44:** 1–15.

Hilzheimer M. 1908. Die Hasenarten Europas. *Jahreshefte des Vereins für vaterl. Naturkund in Wurtt.* **1908:** 383–419.

Hingston RWG. 1932. *A naturalist on the Guiana forest.* New York: Longmans, Green.

Hoffmann RS. 1993. Order Lagomorpha. In: Wilson DE, Reeder DM eds. *Mammal species of the world: a taxonomic and geographic reference*, 2nd edn. Washington: Smithsonian Institution Press, 807–827.

Holley AJ. 1993. Do brown hares signal to foxes? *Ethology* **94:** 21–30.

Honacki JH, Kinman KE, Koeppl JW, eds. 1982. *Mammal species of the world: a taxonomic and geographic reference*. Lawrence, Kansas: Allen Press and the Association of Systematics Collections.

Howell AB. 1929. Mammals from China in the collections of the United States National Museum. *Proceedings of the United States National Museum* **75**.

Huxley J. 1942. *Evolution: the modern synthesis.* New York: Harper and Brown.

Jones KE, Purvis A, MacLarnon A, Bininda-Emonds ORP, Simmons NB. 2002. A phylogenetic supertree of the bats (Mammalia: Chiroptera). *Biological Reviews* **77:** 223–259.

de Jong WW. 1998. Molecules remodel the mammalian tree. *Trends in Ecology and Evolution* **13:** 270–275.

Källersjö M, Farris JS, Kluge AG, Bult C. 1992. Skewness and permutation. *Cladistics* **8:** 275–287.

Kao Y, Feng T. 1964. On the subspecies of the Chinese greytailed hare, *Lepus oiostolus* Hodgson. *Acta Zootaxonomica Sinica* **1:** 19–30.

Kaufman DW. 1974. Adaptive coloration in *Peromyscus polionotus*: experimental selection by owls. *Journal of Mammalogy* **55:** 271–283.

Kiltie RA. 1988. Countershading: universally deceptive of deceptively universal? *Trends in Ecology and Evolution* **3:** 21–23.

Kiltie RA. 1989. Testing Thayer's countershading hypothesis: an image processing approach. *Animal Behavior* **38:** 542–544.

Kluge AG. 1989. A concern for evidence and a phylogenetic hypothesis of relationships among Epicrates (Boidae, Serpentes). *Systematic Zoology* **38:** 7–25.

Koenigswald W. 1996. Die Zahl der Schmelzschichten in den Inzisiven bei den Lagomorpha und ihre systematische Bedeutung. [The number of fusion layers in the incisors of the Lagomorpha and their systematic implications.] *Bonner Zoologische Beiträge* **46:** 33–57. (In German).

Kowalski K, Rzebik-Kowalska B. 1991. *The mammals of Algeria*. Ossolinskich, Wydawn: Polskiej Akademiii Nauk.

Leyhausen P. 1979. *Cat behaviour: the predatory social behaviour of domestic and wild cats*. New York: Garland STPM Press.

Liu F-GR, Miyamoto MM, Freire NP, Ong PQ, Tennant MR, Young TS, Gugel KF. 2001. Molecular and morphological supertrees for eutherian (placental) mammals. *Science* **291:** 1786–1789.

Lorenzo AMC. 1987. Estudio cromosomico comparativo entre las especies de leporidos *Sylvilagus cunicularius, S. floridanus* y *S. graysoni* (Mammalia: Lagomorpha). [Comparative chromosome study between the species of leporids *Sylvilagus cunicularis*, *S. floridanus* and *S. graysoni* (Mammalia: Lagomorpha).] Unpublished B.S. Thesis. Mexico Distrito Federal: Universidad Nacional Autonoma de Mexico. (In Spanish).

Lundholm BG. 1955. Description of new mammals. *Annals of the Transvaal Museum* **22:** 279–303.

Lydekker R. 1907. *The game animals of India, Burma, Malaya, and Tibet*. London: R. Ward.

Lyon MW. 1904. Classification of the hares and their allies. *Smithsonian Miscellaneous Collections* **45:** 321–447.

Ma Y. 1986. *Fauna Heilongjianica Mammalia*. Harbin: Heilongjiang Science and Technology Press.

Maddison WP. 1990. A method for testing the correlated evolution of two binary characters: are gains or losses concentrated on certain branches of a phylogenetic tree? *Evolution* **44:** 539–557.

Maddison WP, Maddison DR. 1992. *MacClade: analysis of phylogeny and character evolution*, Version 3.04. Sunderland, MA: Sinauer Associates.

Meester JAJ, Rautenbach IL, Dippenaar NJ, Baker CM. 1986. *Classification of Southern African mammals*. Pretoria: Transvaal Museum Monograph no. 5.

Merriam CH. 1890. Results of a biological survey of the San Francisco Mountain region and desert of the Little Colorado, Arizona III: Annotated list of mammals, with description of new species. *United States Department of Agriculture, Division of Ornithology and Mammalogy, North American Fauna* **3:** 43–86.

Mickevich MF. 1978. Taxonomic congruence. *Systematic Zoology* **27:** 143–158.

Miller GS. 1912a. *Catalogue of the mammals of Western Europe in the collection of the British Museum*. London: Trustees of the British Museum (Natural History).

Miller GS. 1912b. List of North American land mammals of the United States National Museum, 1911. *Bulletin of the United States National Museum* **79:** 1–455.

Miller GS, Kellog R Jr. 1955. List of North American recent mammals. *Bulletin of the United States National Museum* **205:** 1–954.

Miller GS, Rehn JAG. 1901. Systematic results of the study of North American land mammals to the close of the year 1900. *Proceedings of the Boston Society of Natural History* **30:** 1–352.

Mishler BD. 1994. Cladistic analysis of molecular and morphological data. *American Journal of Physical Anthropology* **94:** 143–156.

Mitchell RM. 1978. The *Ochotona* (Lagomorpha: Ochotonidae) of Nepal. *Säugetierkundliche Mitteilungen* **26:** 208–214.

Monnerot M, Casane D, Hardy C, Vigne J-D. 1994. Evolution of *Oryctolagus*: relationships within the Lagomorpha system and access to population history by ancient data. *Polish Ecological Studies* **20:** 543–551.

Nelson EW. 1907. Descriptions of new North American rabbits. *Proceedings of the Biological Society of Washington* **20:** 81–84.

Nelson EW. 1909. Rabbits of North America. *North American Fauna* **29:** 11–314.

Nixon KC. 1999. The parsimony ratchet, a new method for rapid parsimony analysis. *Cladistics* **15:** 407–414.

Novacek MJ. 1992. Mammalian phylogeny: shaking the tree. *Nature* **356:** 121–125.

Nowak RM. 1999. *Walker's mammals of the world*, 6th edn. Baltimore: John Hopkins University Press.

Ognev SI. 1929. Zur Systematik der russischen Hasen. [On the systematics of Russian hares]. *Zoological Anz.* **84:** 71–73. (In German).

Ognev SI. 1940. *Zveri SSSR i prilezhashchith stran. khishchneyei i lastonogie (Zveri vostochnoi Evropyi severnoi Azii) Mammals of the USSR and adjacent countries (mammals of Eastern Europe and Northern Asia), IV: Rodents.* Moscow-Leningrad: Nauka. (In Russian).

Orr RT. 1940. The rabbits of California. *Occasional Papers California Academy of Sciences* **19:** 1–227.

Ortolani A. 1999. Spots, stripes, tail tips and dark eyes: predicting the function of carnivore colour patterns using the comparative method. *Biological Journal of the Linnean Society* **67:** 433–476.

Ortolani A, Caro TM. 1996. The adaptive significance of coat patterns in carnivores: phylogenetic test of classic hypotheses. In: Gittleman J ed. *Carnivore behaviour, ecology and evolution*, Vol. 2. Ithaca, New York: Cornell University Press, 132–188.

Osgood WH. 1909. A revision of the mice of the American genus *Peromyscus*. *United States Department of Agriculture Biological Survey, North American Fauna* **28**.

Osgood WH. 1932. Mammals of the Kelly-Roosevelts and Delacour Asiatic expeditions. *Field Museum of Natural History (Zoological Series)* **18:** 193–339.

Pagel M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. *Proceedings of the Royal Society of London B* **255:** 37–45.

Palacios FA. 1979. Analysis cromosomico, canga de DNA y electroforesis de las liebras espandas [Chromosome, DNA load and electrophoresis analysis of Spanish hares]. *Donana Acta Vertebrata* **6:** 203–215. (In Spanish).

Palacios FA. 1996. Systematics of the indigenous hares of Italy traditionally identified as *Lepus europeaus* Pallas, 1778 (Mammalia, Leporidae). *Bonner Zoologiche Beitraege* **46:** 59–91.

Pavlinov I, Ya Borisenko AV, Kruskop SV, Yakhontov EI. 1995. Mlekopitayushchie Evrazii II. Non-Rodentia: sistematiko-geograficheskii spravochnik [Mammals of Eurasia: 2. Non-Rodentia. Systematic and geographic handbook.]. *Sbornik Trudov Zoologicheskogo Muzeya* **33:** 1–336. (In Russian).

Pavlinov I, Ya Rossolimo OL. 1987. Sistematika mlekopitayushchikh SSSR. [Systematics of the mammals of the USSR]. *Sbornik Trudov Zoologicheskogo Muzeya* **25:** 1–284. (In Russian).

Peddie DA. 1975. A taxonomic and autecological study of the genus *Pronolagus* in southern Africa. Unpublished MSc. Thesis. University of Rhodesia.

Penny D, Hendy MD. 1986. Estimating the reliability of evolutionary trees. *Molecular Biology and Evolution* **3:** 403–417.

Pérez-Suárez G, Palacios F, Boursot P. 1994. Speciation and paraphyly in Western Mediterranean hares (*Lepus castroviejoi*, *L. europaeus*, *L. granatensis*, and *L. capensis*)

revealed by mitochondrial DNA phylogeny. *Biochemical Genetics* **32:** 423–436.

Petter F. 1959. Éléments d'une révision des liévres africains du sous-genre *Lepus*. [Elements of a revision of African hares of the genus *Lepus*] *Mammalia* **23:** 41–67. (In French).

Petter F. 1961. Eléments d'une révision des lievres européens et asiatiques du sous-genre *Lepus*. [Elements of a revision of European and Asian hares of the genus *Lepus*] *Zeitschrift für Säugetierkunde* **26:** 1–11. (In French).

Petter F. 1963. Nouveaux éléments d'une révision des liévres Africains [New elements of a revision of African hares]. *Mammalia* **27:** 238–255. (In French).

Petter F. 1972. Order Lagomorpha. In: Meester J Setzer HW eds. *The mammals of Africa: an identification manual*. Washington: Smithsonian Institute Press, 1–7.

Pierpaoli M, Riga F, Trocchi V, Randi E. 1999. Species distinction and evolutionary relationships of the Italian hare (*Lepus corsicanus*) as described by mitochondrial DNA sequencing. *Molecular Ecology* **8:** 1805–1817.

Poulton EB. 1890. *The colours of animals: their meaning and use, especially considered in the case of insects.* London: Kegan Paul, Trench, Trübner.

Pringle JA. 1974. The distribution of mammals in Natal. Part 1. Primates, Hyracoidea, Lagomorpha (except *Lepus*), Pholidota and Tubulidentata. *Annals of the Natal Museum* **22:** 173–186.

Pucek Z, ed**. 1981.** *Key for the identification of vertebrates of Poland: mammals*. Washington, DC: Polish. Scientific Publishers (translated and published for the Smithsonian Institution and National Science Foundation).

Purvis A. 1995. A composite estimate of primate phylogeny. *Philosophical Transactions of the Royal Society of London B* **348:** 405–421.

Ragan MA. 1992. Phylogenetic inference based on matrix representation of trees. *Molecular Phylogenetics and Evolution* **1:** 53–58.

Rausch RL. 1953. On the status of some Arctic mammals. *Arctic* **6:** 91–148.

Rausch RL. 1963. A review of the distribution of holarctic recent mammals. In: Gressitt JL ed. *Pacific basin biogeography: a symposium*. Honolulu, Hawaii: Bishop Museum Press, 29–43.

Rautenbach IL. 1982. *Mammals of the Transvaal*. Ecoplan Monograph no. 1. Pretoria: Ecoplan.

Rekovets LI. 1990. Systematics and relationships among pikas of the subgenus *Argyrotona* (*Ochotona*, Lagomorpha). *Vestnik Zoologii* **2:** 37–40.

Roberts A. 1951. *The mammals of South Africa*. Johannesburg: The Mammals of South Africa Book Fund.

Roberts TJ. 1977. *The mammals of Pakistan*. London: Ernest Benn.

Robinson TJ. 1982. Key to the South African Leporidae (Mammalia: Lagomorpha). *South African Journal of Zoology* **17:** 220–222.

Robinson TJ, Dippenaar NJ. 1983a. Observations on the status of *L. saxatilis*, *L. whytei* and *L. crawshayi* in southern Africa. *Acta Zoologica Fennica* **174:** 35–39.

Robinson TJ, Dippenaar NJ. 1983b. Morphometrics of the South African Leporidae. 1. Genus Pronolagus Lyin, 1904. *Koninklijk Museum voor Midden Afrika Tervuren Belgie Annalan Zoologische Wetenschappen* **237:** 43–61.

Robinson TJ, Elder FFB, Chapman JA. 1983. Evolution of chromosomal variation in cottontails, genus *Sylvilagus* (Mammalia: Lagomorpha): *S. aquaticus*, *S. floridanus* and *S. transitionalis*. *Cytogenetics and Cell Genetics* **35:** 216–222.

Robinson TJ, Elder FFB, Chapman JA. 1984. Evolution of chromosomal variation in cottontails, genus *Sylvilagus* (Mammalia: Lagomorpha). 2. *Sylvilagus audubonii, S. idahoensis*, *S. nuttallii* and *S. palustris*. *Cytogenetics and Cell Genetics* **38:** 282–289.

Robinson TJ, Osterhoff DR. 1983. Protein variation and its systematic implication for the South American Leporidae (Mammalia: Lagomorpha). *Animal Blood Groups and Biochemical Genetics* **14:** 139–149.

Ruedas LA. 1998. Systematics of *Sylvilagus* (Lagomorpha: Leporidae) from Southwestern North America. *Journal of Mammalogy* **79:** 1355–1378.

Saint-Girons MCh. 1973. *Les mammiféres de France et du Benelux [The mammals of France and of Benelux].* Paris: Doin. (In French).

Samoil HP, Samuel WM. 1981. Use of Coccidia as indicators of phylogenetic relationships of members of the order Lagomorpha. In: Chapman JA Pursley D eds. *Proceedings of the worldwide furbearer conference.* Frostburg, Maryland: Worldwide Furbeaver Conference Inc. 4–29.

Sanderson MJ, Donoghue MJ. 1989. Patterns of variation in levels of homoplasy. *Evolution* **43:** 1781–1795.

Sanderson MJ, Hufford L. 1996. *Homoplasy: the recurrence of similarity in evolution.* San Diego: Academic Press.

Sanderson MJ, Purvis A, Henze C. 1998. Phylogenetic supertrees: assembling the trees of life. *Trends in Ecology and Evolution* **13:** 105–109.

Schaller GB. 1967. *The deer and the tiger: a study of wildlife in India*. Chicago: University of Chicago Press.

Schneider E, Leipoldt M. 1983. DNA relationships within the genus *Lepus* in S.W. Europe. *Acta Zoologica Fennica* **174:** 31–33.

Selous FC. 1908. *African nature notes and reminiscences*. London: MacMillan.

Shortridge GC. 1934. *The mammals of South West Africa*, **Vol. 1**. London: Heinemann.

Simpson GG. 1945. The principles of classification and a classification of mammals. *Bulletin of the American Museum of Natural History* **85:** 1–350.

Smith AT, Formozov NA, Hoffmann RS, Changlin Z, Erbajeva MA. 1990. The pikas. In: Chapman JA, Flux JEC, eds. *Rabbits, hares and pikas: status conservation action plan*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 14–60.

Smithers RHN. 1971. *The mammals of Botswana.* Museum Memoir no. 4. Salisbury: Trustees National Museum of Rhodesia.

Smithers RHN. 1990. *The mammals of the Southern African subregion*. Pretoria: University of Pretoria.

Smorkatsheva AV, Aristov AA, Aksenova TG. 1990. The structure of ear bones in pikas (*Ochotona*, Lagomorpha). *Proceedings of the Zoological Institute of the USSR Academy of Sciences* **215:** 122–136.

Springer MS, de Jong WW. 2001. Phylogenetics. Which mammalian supertree to bark up? *Science* **291:** 1709–1711.

St. Leger J. 1929. An interesting collection of mammals, with remarkable new species of hare from Uganda. *Annals and Magazine of Natural History* **10:** 290–294.

Stoner CJ, Caro TM, Graham CM. In press. Ecological and behavioral correlates of coloration in artiodactyls: systematic analyses of conventional hypotheses. *Behavioral Ecology*. In press.

Sugimura K. 1990. The Amami rabbit *Pentalagus furnessi*. In: Chapman JA, Flux JEC, eds. *Rabbits, hares and pikas: status survey and conservation action plan*. Gland, Switzerland: International Union for Conservation of Nature and Natural Resources, 140–142.

Surridge AK, Timmins RG, Hewitt GM, Bell DG. 1999. Striped rabbits in Southeast Asia. *Nature (London)* **400:** 726.

Swanepoel P, Smithers RHN, Rautenbach IL. 1980. A checklist and numbering system of the extant mammals of the southern African subregion. *Annals of the Transvaal Museum* **32:** 155–196.

Swofford DL. 1999. *PAUP* Phylogenetic Analysis Using Parsimony (*and other methods)*, *Version* 4. Sunderland, MA: Sinauer Associates.

Tate GHH. 1947. *Mammals of Eastern Asia*. New York: Mac-Millian Company.

Thayer GH. 1909. *Concealing-coloration in the animal kingdom*. New York: MacMillan.

Thenius E. 1969. *Phylogenie der Mammalia Stammesgeschichte der Säugetiere (Einschliesslich der Hominiden) [Phylogeny and the origin of Mammalia (including hominids)]*. Berlin: Walter de Gruyter. (In German).

Thomas O. 1903. On a remarkable new hare from the Cape Colony. *Annals and Magazine of Natural History* **11:** 78–79.

Thomas O. 1922. On some new forms of *Ochotona*. *Annals and Magazine of Natural History* **9:** 187–193.

Thomas O, Hinton MAC. 1923. On mammals collected by Captain Shortridge during the Percy Sladen and Kaffrarian Museum Expeditions to the Orange River. *Proceedings of the Zoological Society of London* **1923:** 483–499.

Tomida Y. 1997. Why has the Amami rabbit been classified in the subfamily Paleolaginae in Japan? *Fossils* **63:** 20–28.

Toschi A. 1965. *Fauna d'Italia VII. Mammalia (Lagomorpha-Rodentia-Carnivora-Artiodactyla-Cetacea)* [Fauna of Italy VII. Mammalia (Lagomorpha – Rodentia – Carnivora – Artiodactyla – Cetacea)]. Bologna: Edizioni Calderini. (In Italian).

Vinogradov BS, Argyropulo AI. 1941. *Fauna SSSR, mtekopitayushie. Opredelitel gryzunov. Fauna of the USSR, mammals. Key to rodents.* Moscow-Leningrad: Nauka. (In Russian).

Vinogradov BS, Gromov IM. **1952**. Gryzuny Fauny SSSR [Rodents. Fauna of the USSR]. *Opredeliteli po faune SSSR, izdavaemye Zoologicheskim istitutom Akademii nauk SSSR* **48**. (In Russian).

Vorontsov NN, Ivanitskaya E Yu. 1973. Comparative karyology of north Palaearctic pikas (*Ochotona*, Ochotonidae, Lagomorpha). *Caryologia* **26:** 213–223.

Waddell PJ, Okada N, Hasegawa M. **1999**. Towards resolving the interordinal relationships of placental mammals. *Systematic Biology* **48:** 1–5.

Weston ML. **1981**. The *Ochotona alpina* complex: a statistical reevaluation. In: Myers K, Macinnes CD eds. *Proceedings of the World Lagomorph Conference*. Guelph, Ontario: Guelph University Press, 73–89.

Weston ML. **1982.** A numerical revision of the genus *Ochotona* (Lagomorpha: Mammalia) and an examination of its phylogenetic relationships. Unpublished PhD Dissertation. Vancouver: University of British Columbia.

White JA. **1991**. North American Leporidae (Mammalia, Lagomorpha) from Late Miocence (Clarendonian) to Latest Pliocene (Blancan). *Journal of Vertebrate Paleontology* **11:** 67–89.

Yom-Tov Y. **1967**. On the taxonomic status of the hares (genus *Lepus*) in Israel. *Mammalia* **31:** 246–259.

Youngman PM. **1965**. Mammals of the Yukon Territory. *National Museums of Canada, National Museum of Natural Sciences, Publications in Zoology* **10:** 1–192.

Yu N, Zheng C, Feng Z. **1992**. [The phylogenetic analysis of the subgenus *Ochotona* of China]. *Acta Theriologica Sinica* **12:** 255–266. (In Chinese).

Yu N, Zheng C, Shi L. **1997**. Variation in mitochondrial DNA and phylogeny of six species of pikas (*Ochotona*). *Journal of Mammalogy* **78:** 387–396.

Yu N, Zheng C, Zhang Y-P, Li W-H. **2000**. Molecular systematics of pikas (genus *Ochotona*) inferred from mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution* **16:** 85–95.

Zhou Y, Xia W. **1981**. [An electrophoretic comparison of the serum protein and hemoglobin in three species of mouse hares a discussion on the systematical position of *Ochotona curzoniae*]. *Acta Theriologica Sinica* **1:** 39–44. (In Chinese).

APPENDIX

Species with a particular trait (see row one) were given a value of '1', while those without the trait were coded as '0'. A '?' was assigned to a species when information on a given trait was unavailable or ambiguous. In the dark and white tail columns, a 'NA' (for not applicable) was assigned to species with no visible tails

Species	Common name	Social	Burrow use	Nocturnal and crepuscular	Diurnal	Subtropics and tropics	Arctic and subarctic	High altitude	Open	Closed	Tundra	Desert	Swamp	Rocky	Grassland and scrubland	Forest and woodland	White tail	Dark tail	White ear tips	Dark ear tips	White ventral	White in winter	Red overall coloration	Grey overall coloration	Pale overall coloration	Dark overall coloration
LEPORIDAE																										
Brachylagus idahoensis	Pygmy rabbit	0	1	1	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0
Bunolagus monticularis	Riverine rabbit	0	1	1	0	0	0	?	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	1	0	0
Caprolagus hispidus	Hispid hare	1	1	1	1	1	0	?	0	1	0	0	1	0	1	1	0	0	0	1	1	0	0	0	0	1
Lepus alleni	Antelope jackrabbit	0	0	0	0	1	0	0	1	0	0	1	0	0	1	0	1	1	1	0	1	0	0	0	1	1
Lepus americanus	Snowshoe hare	0	0	1	0	0	1	?	0	0	0	0	0	0	0	1	1	1	1	0	1	1	1	1	0	0
Lepus arcticus	Arctic hare	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	1
Lepus brachyurus	Japanese hare	1	1	1	0	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	1	1	1	1	0	1
Lepus californicus	Black-tailed jackrabbit	?	?	1	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0	1	1	1	0	1	0	0
Lepus callotis	White-sided jackrabbit	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	1	1	0
Lepus capensis	Cape hare	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	1	0	0	0	?	0	0	0	1	1
Lepus castroviejoi	Broom hare	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	0	1	0	1
Lepus comus	Yunnan hare	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	1	0	1	0	1	0
Lepus coreanus	Korean hare	?	?	?	?	1	0	0	0	0	0	0	0	0	?	0	0	1	?	?	?	?	?	?	?	?
Lepus corsicanus	Italian hare	1	0	1	0	0	0	?	0	1	0	0	0	0	1	1	0	0	0	1	1	0	0	1	1	0
Lepus europaeus	European or Brown hare	1	0	1	1	0	0	0	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	0	0
Lepus fagani	Ethiopian hare	?	?	?	?	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	0
Lepus flavigularis	Tehuantepec jackrabbit	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0	0	1
Lepus granatensis	Iberian hare	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	1	1	0	1	1	1	0
Lepus hainanus	Hainan hare	?	0	1	0	1	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	?	0	0	0	1
Lepus insularis	Black jackrabbit	0	0	1	0	0	0	?	0	0	0	0	0	1	1	0	0	1	0	1	1	0	0	0	0	1
Lepus mandshuricus	Manchurian hare	0	0	1	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	1	1	0	0	1
Lepus nigricollis	Indian or Black-naped hare	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	1	1
Lepus oiostolus	Woolly hare	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
Lepus othus	Alaskan hare	0	1	1	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	1
Lepus pequensis	Burmese hare	0	0	1	0	1	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	1
Lepus saxatilis	Scrub hare	0	0	1	0	1	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	1	1
Lepus sinensis	Chinese hare	0	1	1	0	1	0	0	0	1	0	0	1	0	1	1	0	0	0	0	0	0	1	0	0	0
Lepus starcki	Ethiopian highland hare	?	1	?	1	0	0	1	1	0	0	0	0	?	1	0	0	0	0	1	0	0	1	1	1	1
Lepus timidus	Mountain, Blue or Snow hare	?	0	1	?	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0
Lepus tolai		1	0	?	0	1	0	1	1	?	0	?	?	1	1	1	0	0	0	1	0	0	0	0	1	1
Lepus townsendii	White-tailed jackrabbit	?	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	0	1	0	0
Lepus victoriae	African savanna hare	1	?	1	0	1	0	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	1	0	0
Lepus yarkandensis	Yarkand hare	1	?	1	0	1	0	0	1	0	0	1	0	0	0	0	0	0	0	1	1	0	1	1	1	0
Nesolagus netscheri	Sumatran rabbit	?	1	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0	0	0	1
Oryctolagus cuniculus	European rabbit	1	1	1	0	1	1	0	0	0	0	0	0	1	1	0	1	1	0	1	1	0	0	1	0	0

Scientific name	Common name
Pentalagus furnessi	Amami rabbit
Poelagus marjorita	Bunyoro rabbit
Pronolagus crassicaudatus	Greater red rockhare
Pronolagus randensis	Jameson's red rockhare
Pronolagus rupestris	Smith's red rockhare
Romerolagus diazi	Volcano rabbit
Sylvilagus aquaticus	Swamp rabbit
Sylvilagus audubonii	Desert or Audubon's cottontail
Sylvilagus bachmani	Brush rabbit
Sylvilagus brasiliensis	Forest rabbit or Tapeti
Sylvilagus cunicularius	Mexican cottontail
Sylvilagus dicei	Dice's cottontail
Sylvilagus floridanus	Eastern cottontail
Sylvilagus graysoni	Tres Marias cottontail
Sylvilagus insonus	Omilteme cottontail
Sylvilagus mansuetus	San Jose Brush rabbit
Sylvilagus nuttallii	Mountain or Nuttall's cottontail
Sylvilagus palustris	Marsh rabbit
Sylvilagus transitionalis	New England cottontail

OCHOTONIDAE

Scientific name	Common name
Ochotona alpina	Alpine or Altai pika
Ochotona cansus	Gansu or Grey pika
Ochotona collaris	Collared pika
Ochotona curzoniae	Black-lipped or Plateau pika
Ochotona dauurica	Daurian pika
Ochotona erythrotis	Red-eared or Chinese Red pika
Ochotona forresti	Forrest's pika
Ochotona gaoligongensis	Gaoligong pika
Ochotona gloveri	Glover's pika
Ochotona himalayana	Himilayan pika
Ochotona hyperborea	Northern or Siberian pika
Ochotona iliensis	Ili pika
Ochotona koslowi	Kozlov's pika
Ochotona ladacensis	Ladak pika
Ochotona macrotis	Large-eared pika
Ochotona muliensis	Muli pika
Ochotona nubrica	Nubra pika
Ochotona pallasi	Pallas's pika
Ochotona princeps	American pika
Ochotona pusilla	Steppe or Little pika
Ochotona roylei	Royle's pika
Ochotona rufescens	Afghan pika
Ochotona rutila	Turkestan red pika
Ochotona thibetana	Moupin pika
Ochotona thomasi	Thomas's pika