Conserving Mammals at Risk: The Role of Taxonomy

David W. Nagorsen
Royal British Columbia Museum
P.O. Box 9815, STN PROV GOVT, Victoria, BC, V8W 9W2, Canada
Dnagorsen@RBML01.rbcm.gov.bc.ca

Mark A. Fraker
TerraMar Environmental Research Ltd.
8617 Lochside Drive, Sidney, BC, V8L 1M8, Canada

Nick Panter
Royal British Columbia Museum
P.O. Box 9815, STN PROV GOVT, Victoria, BC, V8W 9W2, Canada

ABSTRACT

A number of mammalian species, subspecies, and populations are designated at risk both nationally and by the province of British Columbia. Despite the perception that the taxonomy of mammals is well known, major taxonomic problems are associated with some of these taxa. Species limits and reliable identification traits need to be determined for several problematic species groups. Moreover, the validity of many of the subspecies listed at risk is unknown. Some were described more than 50 years ago from small samples and descriptive methodology, and modern research is essential to determine if they represent distinct evolutionary units that warrant protection. We use recent research on listed subspecies of chipmunks (*Tamias* spp.), northern pocket gophers (*Thomomys talpoides*), and southern red-backed voles (*Clethrionomys gapperi*) from the Kootenay region of British Columbia to illustrate how taxonomy is critical for delimiting conservation units. Preliminary results suggest that the 2 subspecies of the red-tailed chipmunk, *Tamias ruficaudus* (*T. r. simulans*, *T. r. ruficaudus*) are full species. Similarly, the 2 allopatric subspecies of the least chipmunk, *Tamias minimus* (*T. m. selkirki*, *T. m. oreocetes*) appear to be strongly differentiated from other populations, warranting recognition as distinct evolutionary units. In contrast, the Wynndel subspecies (*T. t. segregatus*) of the northern pocket gopher is probably a localized population of *T. t. saturatus* with minor differentiation attributable to genetic drift. Gale's race (*C. g. galei*) of the southern red-backed vole is even more dubious and demonstrates the problems in delimiting discrete units in widespread species with continuous distributions. Comparable modern studies could be applied to most of the subspecies currently listed at risk. A high priority provincially should be the allopatric endemic taxa that inhabit coastal islands or isolated mainland habitats.

Key words: *Clethrionomys gapperi*, least chipmunk, northern pocket gopher, red-tailed chipmunk, southern red-backed vole, *Tamias minimus*, *Tamias ruficaudus*, taxonomy, *Thomomys talpoides*.

Taxonomy, the theory and practice of classifying organisms (Mayr and Ashlock 1991), plays a central role in conserving biodiversity and species at risk. The most important contribution of taxonomy to conservation biology is defining the taxonomic units that we are trying to protect, such as species or subspecies. The definition and biological concepts of species and subspecies and their value as evolutionary significant units (ESUs) in conservation biology has promoted considerable debate among taxonomists and conservation biologists (O'Brien and Mayr 1991, Rojas 1992, Engstrom et al. 1994).

Nationally, the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) has designated 30 mammalian taxa (18 species, 12 subspecies or populations) as either Endangered, Threatened, or Vulnerable (COSEWIC 1999). According to the most recent Red and Blue lists released by the British Columbia Ministry of Environment, Lands and Parks (Cannings et al. 1999), the province recognizes 49 mammalian taxa at risk in British Columbia: 22 species and 27 subspecies. Although mammals as a group are generally regarded as well understood taxonomically, much of the taxonomy supporting these listings is dated and largely the result of research done 50 to 100 years ago. The number of valid species is unclear for several groups such as the long-eared myotis bats (*Myotis evotis*, *M. keenii*, *M. septentrionalis*), and the chipmunks (*Tamias* spp.). Taxonomy at the subspecies level is even more uncertain. COSEWIC's national designations of even high-profile, large mammals such as the gray wolf (*Canis lupus*), grizzly bear (*Ursus arctos*), and caribou (*Rangifer tarandus*) have been hampered by taxonomic controversies. The 27 mammalian subspecies listed by the province are also problematic, with most described from subjective methods using

L. M. Darling, editor. 2000. Proceedings of a Conference on the Biology and Management of Species and Habitats at Risk, Kamloops, B.C., 15 - 19 Feb.,1999. Volume One.
B.C. Ministry of Environment, Lands and Parks, Victoria, B.C. and University College of the Cariboo, Kamloops, B.C. 490pp.

Table 1. Red and Blue List status of 6 rodent subspecies at risk from the Kootenay region of southeastern British Columbia.

Common name	Scientific name	Status
Red-tailed chipmunk (Rocky Mountain ssp.)	*Tamias ruficaudus ruficaudus*	Red
Red-tailed chipmunk (Selkirk ssp.)	*Tamias ruficaudus simulans*	Red
Least chipmunk (Timberline ssp.)	*Tamias minimus oreocetes*	Red
Least chipmunk (Selkirk ssp.)	*Tamias minimus selkirki*	Red
Northern pocket gopher (Wynndel ssp.)	*Thomomys talpoides segregatus*	Red
Southern red-backed vole (Gale's ssp.)	*Clethrionomys gapperi galei*	Blue

inadequate sample sizes. Their validity as distinct evolutionary significant units that should be protected and conserved is unknown. A few of the listed subspecies may be full species but most are dubious.

Many of these taxonomic problems are the legacy of early taxonomic research on North American mammals. Early taxonomists operated with a typological species concept. They had little appreciation of geographic variation, and virtually every mammalian population with minor differences was described as a new species (Engstrom et al. 1994). This was followed by taxonomists adopting the polytypic species concept (Mayr and Ashlock 1991), where species are recognized as being geographically variable, and distinct geographic forms are formally treated under the Code of Zoological Nomenclature as subspecies with a trinomen. This led to numerous taxonomic revisions, with many species being reduced to the subspecies level. However, in most of these revisions taxonomists tended to retain the original species names as subspecies. Often "species" were simply reduced to subspecies with no rigorous studies of geographic variation to substantiate that they were in fact taxonomically different. Many of these subspecies persist today and are listed in standard synoptic references such as Cowan and Guiguet (1965), Banfield (1974), Hall (1981), and Nagorsen (1990). Whatever conceptual basis is applied to define species or subspecies, modern taxonomic classifications are based on detailed studies of geographic variation applying rigorous quantitative techniques with morphological and molecular data. Few such modern studies have been done on Canada's mammalian fauna.

In this paper we review results from our taxonomic research on 6 subspecies representing 4 provincially listed rodent species (Table 1) from the Kootenay region of southeastern British Columbia. We use these taxa as case studies to explore some of the issues concerning taxonomy and conservation. It should be emphasized that our results are based on small samples and are preliminary.

METHODS

In 1996, the Columbia Basin Fish and Wildlife Compensation Program, the Ministry of Environment, Lands and Parks, the Royal British Columbia Museum, and Terramar Environmental Research Ltd. initiated a collaborative study to investigate the taxonomy, distribution, and conservation status of 6 taxa of small mammals from the Kootenay region. Taxonomic analyses are based on voucher specimens collected from 1996 to 1998. In 1996, voucher samples included southern red-backed voles (*Clethrionomys gapperi*) and chipmunks (*Tamias* spp.) from the Akamina-Kishinena region of the southern Rocky Mountains, chipmunks from the southern Selkirk Mountains, and northern pocket gophers (*Thomomys talpoides*) from the Creston Valley. The 1997 field studies concentrated on chipmunks from the Purcell Mountains and adjacent areas in the Rocky Mountain trench; 1998 field studies concentrated on chipmunk samples from the southern Rocky Mountains and Purcell Mountains. Detailed information on sampling sites and vouchers specimens were summarized by Nagorsen (1997), Fraker and Nagorsen (1998), and Nagorsen and Fraker (1999). Our voucher samples were augmented with historical museum specimens taken in the Kootenay region.

Our analyses were heavily based on genital bone morphology, an important taxonomic and identification trait in chipmunks. All voucher specimens were identified to species from genital bone preparations. Identification of historical museum specimens was verified from radiographs of study skins that revealed genital bones. Canonical variate analyses based on 8 male genital bone measurements and 15 cranial measurements were used to assess geographic variation. Samples of the red-tailed chipmunk (*T. ruficaudus*) were too small for rigorous statistical analysis, and only results for the least chipmunk (*T. minimus*) are shown. For details on the taxonomic analyses of chipmunks see Fraker and Nagorsen (1998) and Nagorsen and Fraker (1999).

Nagorsen (1997) summarized the techniques used to assess variation in skull shape and pelage colour of *T. talpoides*. We analyzed 10 samples representing 7 subspecies from western Canada. Results are shown for females. Because size is highly plastic in pocket gophers we removed size effects from the data with the Burnaby shearing technique (Rohlf and Bookstein 1987) and examined patterns of variation in skull shape with a canonical variate analysis of 8 skull measurements. Studies on a related species in California have shown that patterns of variation defined by skull shape may be concordant with genetic variation (Smith

and Patton 1988). We scored the degree of white spotting of the pelage from 4 ventral regions of museum study skins: chin, chest, forearms, and abdomen. Each area was ranked from 0 (no spotting) to 3 (heavy spotting) for the degree of spotting and scores were totalled for an overall spotting index of each specimen.

Our analysis of *C. gapperi* was restricted to a superficial comparison of our vouchers with historical museum specimens and a review of the published descriptions for the 8 subspecies recognized in British Columbia. No quantitative analyses were done.

CASE STUDIES

Red-tailed Chipmunk (*Tamias ruficaudus*)

T. ruficaudus is an example of a species-level problem. Two subspecies are currently recognized: *T. r. ruficaudus* associated with the Rocky Mountains of Montana, Idaho, and southern British Columbia; and *T. r. simulans* associated with the Selkirk Mountains of eastern Washington, northern Idaho, and southern British Columbia (Fig. 1). From a study of bacular (i.e., male genital bone) morphology in populations from Washington, Idaho, and Montana, Patterson and Heaney (1987) suggested that the 2 taxa are full species. Preliminary results of an analysis of our voucher specimens and known museum specimens from western Canada demonstrate that at the northern periphery of their range in Canada, the 2 subspecies differ in pelage, skull, and genital bone morphology. The 2 taxa also show ecological differences, with *T. r. ruficaudus* confined to the subalpine (1,800–1,900 m) in the Rocky Mountains, whereas the known range of *T. r. simulans* is from 700 to 1,830 m in the Selkirk Mountains. Cowan and Guiguet (1965) and Hall (1981) showed the 2 subspecies in contact in the Purcell Mountains and Rocky Mountain trench. However, recent field studies and an examination of historical museum specimens have revealed that *T. ruficaudus* is absent from the Purcell Mountains. Thus, the distributions of *T. r. ruficaudus* and *T. r. simulans* in Canada appear to be allopatric, with the 2 taxa separated by the Creston Valley, the Rocky Mountain trench, and the intervening Purcell Mountains (Fig. 1). All of these data support the recognition of *T. r. ruficaudus* and *T. r. simulans* as full species. Molecular research now being done by Jack Sullivan in Idaho where the 2 groups may be in contact should resolve the species question.

Both *T. r. ruficaudus* and *T. r. simulans* are listed on the provincial Red List at the subspecies level, and, from a conservation perspective, debates about differentiation at the species versus subspecies level may appear academic. However, a listed species has higher conservation priority than a listed subspecies. More importantly, most of what is known of the biology of *T. ruficaudus* is based on studies of *T. r ruficaudus* done in Montana (Beg 1969) and Beg's data may not be relevant to *T. r. simulans*, particularly if it is a different species.

Least Chipmunk (*Tamias minimus*)

T. minimus is represented by 4 subspecies in British Columbia (Fig. 2). The northern subspecies, *T. m. borealis* and *T. m. caniceps*, are widespread; in contrast, *T. m selkirki* and *T. m. oreocetes* are alpine races found above 1,900 m. *T. m. selkirki* was described and named by Cowan (1946) from only 5 specimens taken from the type locality at Paradise Mine in the Purcell Mountains. Our field surveys in 1997 (Fraker and Nagorsen 1998) and 1998 (Nagorsen and

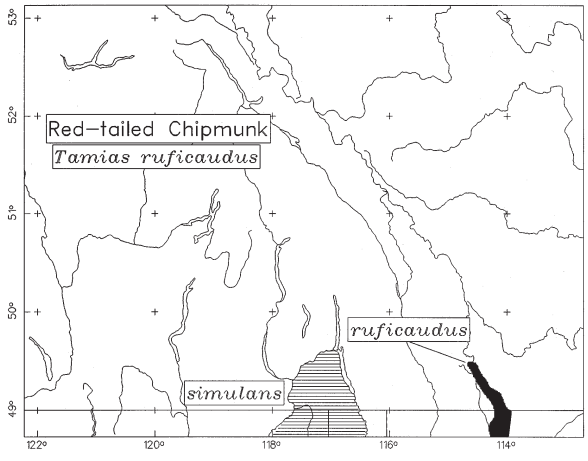

Figure 1. Distribution of the 2 subspecies of the red-tailed chipmunk (*Tamias ruficaudus*) in Canada.

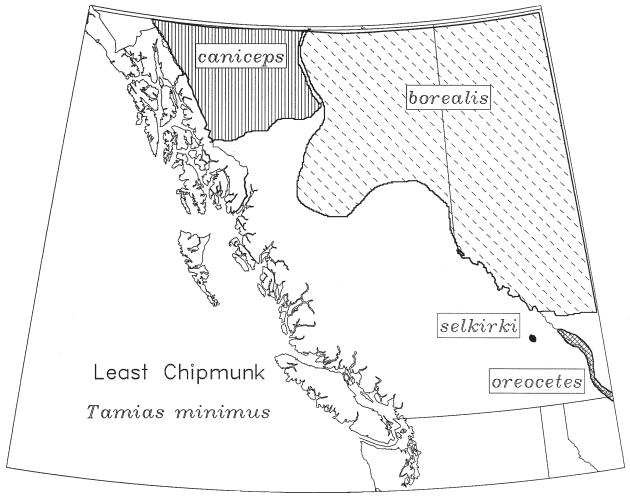

Figure 2. Distribution of the 4 subspecies of the least chipmunk (*Tamias minimus*) in British Columbia and western Alberta.

Fraker 1999) added a few new locations, but this taxon is still known from only a very restricted area. *T. m. oreocetes*, a small pale form described by Merriam (1897), occupies the Rocky Mountains of southern Canada and northern Montana. Taxonomic validity of these races is not clear and the precise distribution of *T. m. oreocetes* in Canada is contentious. Cowan (1946) concluded that it was restricted to the Waterton Lakes area in Canada, but Crowe (1943) assigned *T. minimus* from as far north as Mount Assiniboine Provincial Park and Tornado Pass to *T. m. oreocetes*, a hypothesis supported by Banfield (1958).

Our analyses demonstrate that *T. m. selkirki* is strongly differentiated from both *T. m. oreocetes* and *T. m. borealis* in male bacular bone morphology (Fig. 3). A similar pattern of variation was found in our analysis of cranial morphology. The strong differentiation of *T. m. selkirki* from *T. m. oreocetes*, despite their geographic proximity, is significant. These 2 alpine populations, separated by the Rocky Mountain trench and lowland populations of the yellow pine chipmunk (*T. amoenus*), have probably been isolated since the early postglacial. Although *T. m. oreocetes* also appears to be morphologically distinct, its taxonomic status and distribution are unresolved and more samples are needed. The small, pale form of *T. minimus* in the southern Canadian Rocky Mountains may represent 1 extreme in a north-south cline that extends along the Canadian Rocky Mountains. Cowan (1946) described clinal variation in body measurements among northern *T. m. borealis* and the southern *T. m. oreocetes.* However, if *T. m. borealis* and *T. m. oreocetes* are separated by the Bow River and lowland populations of *T. amoenus* in Banff National Park, as suggested by Banfield (1958), then it is possible that a sharp step-cline delimiting these 2 subspecies could occur across the Bow River. Our results are based on a sample of only 3 *T. m. oreocetes* specimens from Alberta. A comprehensive study based on all historical museum specimens and new material taken in August 1998 is in progress.

The extent to which these chipmunk subspecies are at risk is not clear. If taxonomic studies demonstrate that *T. m. oreocetes* ranges as far north as the Bow River in Canada, then much of the Canadian range of this taxon falls in national and provincial parks and it may be appropriate to downlist its ranking. Because its known distributional area is small and isolated from other populations, *T. m. selkirki* is more likely to be at risk and it was recently listed as Vulnerable by the International Union for the Conservation of Nature (IUCN; Sullivan and Nagorsen 1998).

Northern Pocket Gopher (*Thomomys talpoides*)

A fossorial mammal that spends much of its life underground, the distribution of *T. talpoides* is fragmented by areas of unsuitable soil and physical barriers such as rivers and lakes. The pocket gophers are the most morphologically and genetically variable of all mammals and some 58 subspecies have been described for *T. talpoides,* most defined by minor differences in fur colour (Hall 1981). This excessive naming of every local variant in pocket gophers has been singled out as an example of a misuse of the subspecies concept (Simpson 1961).

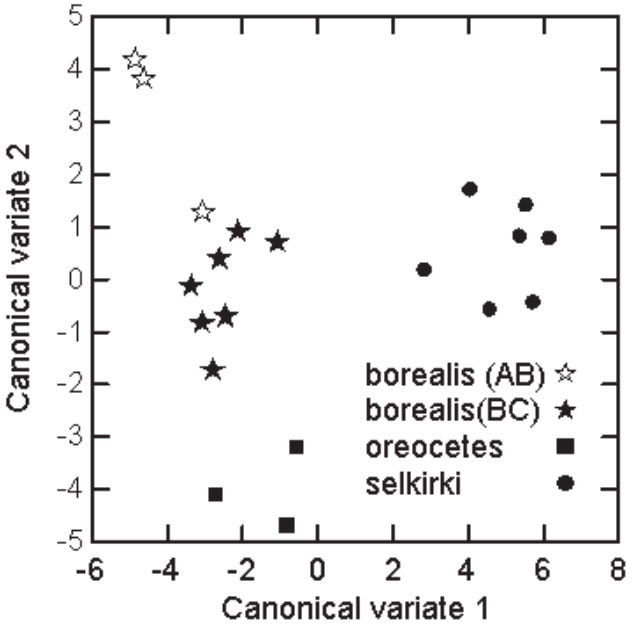

Figure 3. Projection of 4 groups of least chipmunks (*Tamias minimus*) representing 3 subspecies on the first 2 canonical variates derived from 8 bacular bone measurements.

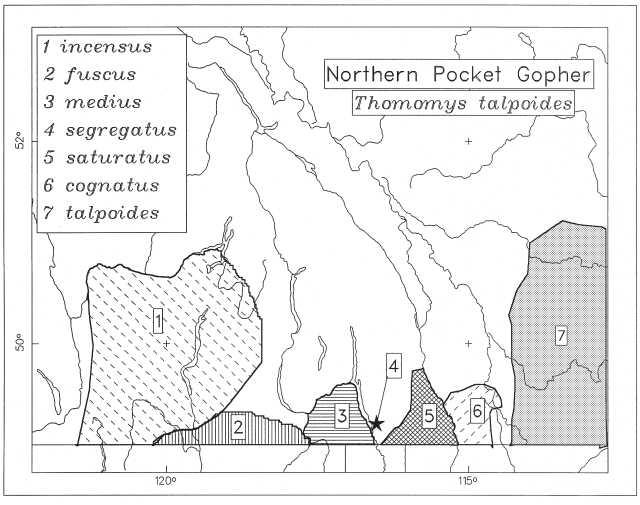

Figure 4. Distribution of 7 subspecies of the northern pocket gopher (*Thomomys talpoides*) in British Columbia and western Alberta.

Taxonomy of the British Columbian populations was last revised by Johnstone (1954). Using largely descriptive methodology, he recognized 6 subspecies (Fig. 4) including 2 previously undescribed subspecies, and argued that they were maintained by the isolating effects of the Columbia and Kootenay rivers. Based on a comprehensive inventory, Fraker et al. (1997) found that *T. t. segregatus,* the isolated race found near Wynndel above the Kootenay floodplain north of Creston, still occupies the same 10-km^2 area that it did 50 years ago when first discovered by Munro (1950). Even though *T. t . saturatus* invaded the southern Creston Valley from Idaho in the 1960s, *T. t . saturatus* and *T. t . segregatus* are allopatric in British Columbia, with their distributions separated by about 13 km (Fraker et al. 1997). Because of its small population size and isolation, *T. t. segregatus* is susceptible to extinction from stochastic events. However, the fundamental issue is whether this population represents a distinct taxonomic unit or is simply a local variant of an adjacent subspecies such as *T. t. saturatus* or *T. t. medius*, with minor differences that can be attributed to genetic drift in a localized population.

Our analyses of 10 samples representing 7 subspecies from western Canada, demonstrated that the prairie race *T. t. talpoides* from southwestern Alberta falls out as a distinct group (Fig. 5). The 6 races from British Columbia overlap on the first axis, but there is some separation on the second axis, with samples from the Kootenays at the top and samples from the Okanagan-Cascades at the bottom. Nonetheless, the morphological data provide little evidence for 6 distinct groups in the province and, most significantly, the Wynndel subspecies *T. t. segregatus* does not fall out clearly as a distinct form.

The incidence of the white spotting mutation is variable within and among the 10 populations (Fig. 6) with no strong concordance with subspecies. However, this coat colour mutant is most prevalent in *T. t. segregatus*. The strong differences in this mutation exhibited by the Wynndel population and the sample of *T. t. medius* from the west side of the Creston Valley is striking and supports the hypothesis of Johnstone (1954) and Fraker et al. (1997) that the Kootenay River and floodplain form a formidable barrier to pocket gopher dispersal and gene flow.

Although the use of subspecies is controversial, particularly for highly variable taxa such as pocket gophers, Smith and Patton (1988) supported the concept if the subspecies reflect evolutionary units that share similar morphological and genetic traits. Despite their support for subspecies, Smith and Patton (1988) recommended that local variants attributable to genetic drift in small populations do not warrant subspecific status. *T. t. segregatus* could be a relict population resulting from an early postglacial invasion of British Columbia or it may be a recent isolate of *T. t . saturatus*,

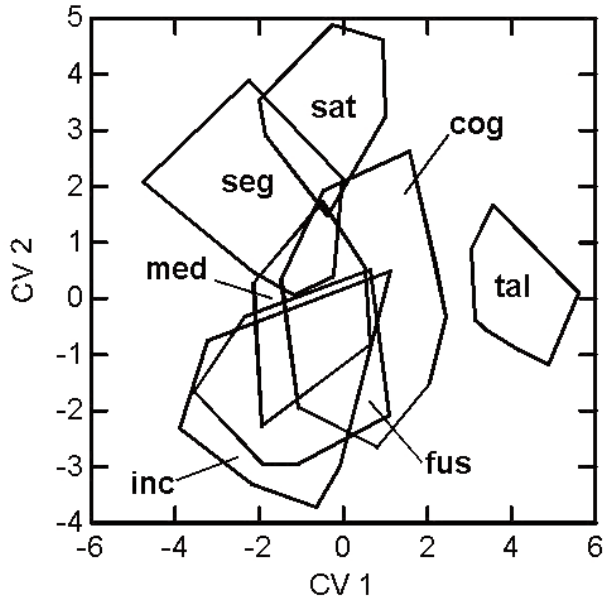

Figure 5. Projection of 7 subspecies of the northern pocket gopher (*Thomomys talpoides*) on the first 2 canonical variates derived from 8 size-corrected skull measurements. Polygons enclose the outermost points of each subspecies. (cog = *cognatus*; fus = *fuscus*; inc = *incensus*; med = *medius*; sat = *saturatus*; seg = *segregatus*; tal = *talpoides*.)

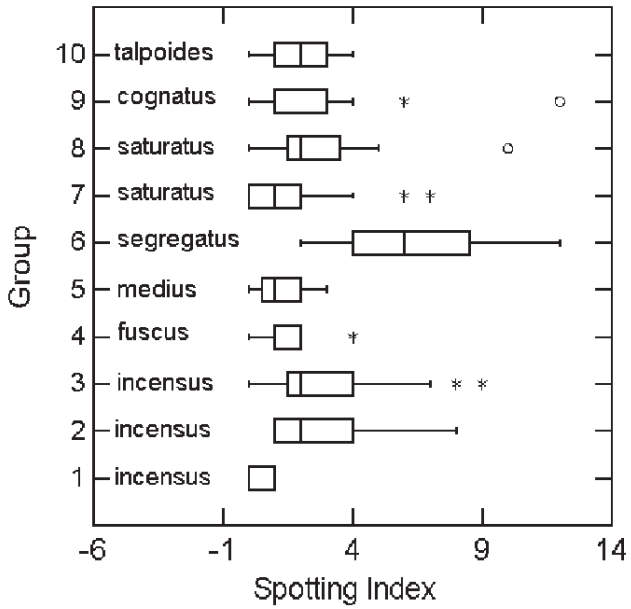

Figure 6. Box plots showing the degree of white spotting in 10 samples representing 7 subspecies of the northern pocket gopher (*Thomomys talpoides*). Vertical line is the median; the box delimits the hinges (1st and 3rd quantiles); stars and open circles indicate outliers.

with most of its divergence (the white spotting and minor differentiation in skull morphology) attributable to drift in a small isolated population. Only genetic studies (chromosomes, allozymes, DNA) will clarify the taxonomy of *T. talpoides*. If it is revealed that *T. t segregatus* is not a valid subspecies and it is synonymized with another race, such as *T. t. saturatus*, which is not at risk, then *T. talpoides* would simply disappear from the provincial Red List. However, until such taxonomic studies are done it is prudent to maintain *T. t segregatus* on the provincial Red List. In a recent IUCN conservation action plan for North American rodents this subspecies was designated as "Lower Risk, near threatened" with a recommendation for a modern taxonomic study of the species (Yensen and Nagorsen 1998).

SOUTHERN RED-BACKED VOLE (*CLETHRIONOMYS GAPPERI*)

C. gapperi illustrates the problem of delimiting subspecies in species with a continuous distribution. Eight subspecies are recognized in the province (Fig. 7). *C. g. galei*, a widespread race found in the Rocky Mountains of the United States, barely enters the southeast corner of the province. It is appears on the provincial Blue List, presumably because of few locality records, although the species seems abundant and widespread in the southern Canadian Rocky Mountains (Fraker and Nagorsen 1998). Another subspecies, *C. g. occidentalis*, occupies the Puget Sound lowlands of Washington Sate and the extreme southwestern edge of the Fraser Valley. Known in the province from only 2 historical records in the Vancouver area, this taxon is Red-listed and may be extirpated in British Columbia. However, there has been no modern taxonomic revision of *C. gapperi* and most of the named subspecies are a legacy of early species descriptions. Both *C. g. galei* and *C. g. occidentalis* were originally described as species by Merriam (1890) under the old generic name *Evotomys* based on vague descriptive traits taken from only a few specimens. For example, Merriam's description of *Evotomys* (= *Clethrionomys*) *galei* as a new species was based solely on a single specimen—the type specimen taken from Boulder Colorado. His original description consists of vague statements such as: "size about equal to that of *E. gapperi*, or larger,….above considerably lighter than true *gapperi*,…the molar series are considerably larger than in skulls of *gapperi* of the same size…" The last major taxonomic revision of North American forms of *Clethrionomys* was done more than 100 years ago by Bailey (1897). The group is clearly in need of a modern taxonomic revision.

As part of the Kootenay small mammal project we were asked to determine the validity of *C. g. galei* using the few voucher specimens taken during the 1996 inventory and existing museum specimens from the Kootenay region. However, to resolve the subspecies taxonomy of *C. gapperi* requires a major taxonomic study across western North America, assessing geographic variation in morphological and genetic traits. Several distinct taxonomic units of *C. gapperi* probably occur in British Columbia, but it is unlikely that they will be concordant with the 8 subspecies currently recognized. Because it is abundant, ecologically widespread, and contiguous with other subspecies such as *C. g. saturatus*, we recommend that *C. g. galei* be removed from the provincial list of vertebrates at risk. *C. g. occidentalis* and other coastal subspecies (*phaeus*, *stikinensis*, *caurinus*, *cascadensis*) probably represent a single coastal evolutionary unit. However, until the taxonomy is revised, it is appropriate to continue to treat *C. g. occidentalis* as a taxon at risk.

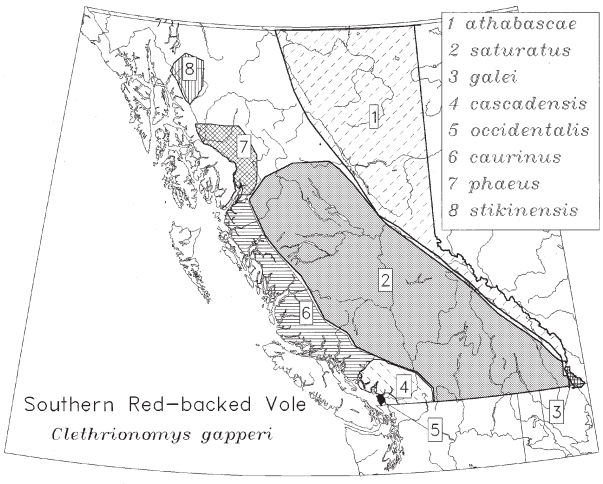

Figure 7. Distribution of the 8 subspecies of the southern red-backed vole (*Clethrionomys gapperi*) in British Columbia.

DISCUSSION

The small mammals from the Kootenay region selected for our study support our hypothesis that many of the taxonomic units of mammals currently listed at risk are the product of dated and invalid taxonomy. The *T. ruficaudus* example demonstrates that species-level problems still exist with some Canadian mammals. Our support for recognizing the 2 subspecies (*T. r. ruficaudus* and *T. r. simulans*) as full species is consistent with the prediction of Engstrom et al. (1994) that the number of North American mammal species will increase with additional taxonomic research. Evidently a number of sibling species were reduced to the subspecies level in the wave of taxonomic revisions that followed the use of the polytypic species concept. Most taxonomic problems for listed mammals are associated with subspecies and populations. Modern taxonomic techniques will undoubtedly confirm the validity of some of these taxa. Despite the small sample sizes and descriptive methodology used by Cowan (1946), our

findings support Cowan's conclusions and strengthen the case for treating *T. m. selkirki* as a distinct taxonomic unit of the least chipmunk. However, many subspecies, particularly in species with continuous distributions such as *C. gapperi*, are of dubious taxonomic validity. The trend over the past few decades has been a reduction in the number of accepted subspecies for North American mammals (Engstrom et al. 1994). Modern taxonomic revisions may reduce the lists of subspecies at risk through synonomy.

Although most of our focus has been on verifying taxa already named and described, it is conceivable that there are well-defined taxonomic units of mammals that have yet to be identified. Limited data on yellow-pine chipmunks (*Tamias amoenus*) from the Kootenay region suggest that populations on the west and east sides of the Rocky Mountain trench differ strikingly in male bacular bone morphology (Fraker and Nagorsen 1998). Although populations from the Kootenay region are currently assigned to a single subspecies, *T. a. luteiventris* (Cowan and Guiguet 1965), this taxon may consist of several strongly differentiated groups. Thus significant taxonomic diversity may be concealed within some recognized taxa.

Resolving these taxonomic problems is a major task that must be done on a species by species basis by applying powerful modern tools including molecular techniques and numerical analysis of traditional morphological traits. However, with few funds and taxonomists available, little taxonomic research is being done on Canada's mammalian fauna. In 1993 Canada's national museum, the Canadian Museum of Nature, eliminated its mammalogist position and research program in mammalian systematics. Provincially in British Columbia, the Royal British Columbia Museum struggles with tight budgets and limited resources. No mammalian taxonomists are on staff at any of the province's universities. Provincial funding for the province's Red- and Blue-listed mammals has been directed at field inventory and habitat studies rather than verification of the taxonomic validity of the listed taxa.

A taxonomic assessment of every mammalian taxa listed nationally or provincially is clearly not feasible or warranted. Provincially, a high priority should be the allopatric, endemic taxa. Endemic taxa warrant special concern because they occur nowhere else. Allopatric populations are more likely to be differentiated taxonomically because of isolation and restricted gene flow. This isolation also makes them vulnerable to extinction because there is little opportunity for a rescue effect. A few allopatric, endemic mammalian taxa (e.g., *T. m. selkirki*) occur in isolated mainland habitats of British Columbia, but most are associated with the numerous coastal islands (Nagorsen 1990). Research now being done on the insular mammals of southeast Alaska (MacDonald and Cook 1996) is a model for the kind of research that needs to be done in British Columbia.

ACKNOWLEDGEMENTS

Our research was supported by the Royal British Columbia Museum, the Columbia Basin Fish and Wildlife Compensation Program, Forest Renewal British Columbia, and the British Columbia Ministry of Environment, Lands and Parks. We thank J. Krebs, T. Antifeau, and L. Ingham for their strong support. Our chipmunk research benefited from discussions with I. McTaggart Cowan. The Canadian Museum of Nature; Cowan Vertebrate Museum, University of British Columbia; Museum of Zoology, University of Alberta; Provincial Museum of Alberta; and Royal Ontario Museum provided loans of chipmunk specimens and allowed one of us (DWN) to measure pocket gopher specimens in their collections.

LITERATURE CITED

Bailey, V. 1897. Revisions of American voles of the genus *Evotomys*. Proc. Biol. Soc. of Washington 11:113–138.

Banfield, A. W. 1958. The mammals of Banff National Park, Alberta. Natl. Mus. of Can., Ottawa, ON. Bull. 57, 159:1–53.

_____. 1974. The mammals of Canada. University of Toronto Press, Toronto, ON.

Beg, M. A. 1969. Habitats, food habits, and population dynamics of the red-tailed chipmunk, *Eutamias ruficaudus*, in western Montana. Ph.D. thesis, Univ. Montana, Missoula, MT.

Cannings, S. G., L. R. Ramsay, D. F. Fraser, and M. A. Fraker. 1999. Rare amphibians, reptiles, and mammals of British Columbia. Wildl. Branch and Resour. Inventory Branch, B.C. Minist. Environ., Lands and Parks, Victoria, BC.

COSEWIC. 1999. List of Canadian species at risk, April 1999. Comm. on Status of Endangered Wildl. in Can., Ottawa, ON.

Cowan, I. M. 1946. Notes on the distribution of the chipmunks (*Eutamias*) in southern British Columbia and the Rocky Mountain region of southern Alberta with descriptions of two new races. Proc. Biol. Soc. of Washington 59:107–118.

_____, and C. J. Guiguet. 1965. The mammals of British Columbia. B.C. Prov. Mus., Victoria, BC. Handb. 11.

Crowe, P. E. 1943. Notes on some mammals of the southern Canadian Rocky Mountains. Bull. Amer. Mus. Nat. Hist. 80:391–410.

Engstrom, M. D., J. R. Choate, and H. H. Genoways. 1994. Taxonomy. Pp. 179–199 *in* E. C. Birney, and J. R. Choate, eds. Seventy-five years of mammalogy (1919-1994). Amer. Soc. Mammal., Lawrence, KS. Spec. Publ. 11.

Fraker, M. A., and D. W. Nagorsen. 1998. Chipmunks (*Tamias*) and southern red-backed voles (*Clethrionomys gapperi*) in the Kootenay region of southeastern British Columbia: results of 1996 field studies. TerraMar

Environmental Research, Sidney, BC. Unpubl. rep.

_____, B. A. Sinclair, D. Joly, and M. V. Ketcheson. 1997. Distribution and habitat associations of northern pocket gophers (*Thomomys talpoides*) in the Creston Valley, B.C. TerraMar Environmental Research, Sidney, BC. Unpubl. rep.

Hall, E. R. 1981. The mammals of North America, Second edition, Vol. 1-2. Wiley and Sons, New York, NY.

Johnstone, W. B. 1954. A revision of the pocket gopher *Thomomys talpoides* in British Columbia. Can. Field-Nat. 68:155–164.

MacDonald, S. O., and J. A. Cook. 1996. The land mammal fauna of southeast Alaska. Can. Field-Nat. 110:571–598.

Mayr, E., and P. D. Ashlock. 1991. Principles of systematic zoology. McGraw-Hill, New York, NY.

Merriam, C. H. 1890. Descriptions of twenty-six new species of North American mammals. North Amer. Fauna 4:1–60.

_____. 1897. Notes on the chipmunks of the genus *Eutamias* occurring west of the east base of the Cascade-Sierra system. Proc. Biol. Soc. of Washington 11:189–212.

Munro, J. A. 1950. The birds and mammals of the Creston region, British Columbia. B.C. Prov. Mus., Victoria, BC. Occas. Pap. 8:1–89.

Nagorsen, D. W. 1990. The mammals of British Columbia. A taxonomic catalogue. Roy. B.C. Mus., Victoria, BC. Mem. 4:1–140.

_____.1997. Kootenay small mammal project. Part 2: taxonomy and identification. Roy. B.C. Mus., Victoria, BC. Unpubl. rep.

_____, and M. A. Fraker. 1999. Chipmunks (*Tamias*) in the Kootenay region of southeastern British Columbia: results of 1998 field studies. Columbia Basin Fish and Wildl. Compensation Prog., Nelson, BC. Unpubl. rep.

O'Brien, S. J., and E. Mayr. 1991. Bureaucratic mischief: recognizing endangered species and subspecies. Science 25:1187–1188.

Patterson, B. D., and L. R. Heaney. 1987. Preliminary analysis of geographic variation in red-tailed chipmunks (*Eutamias ruficaudus*). J. Mammal. 68:782–791.

Rohlf, F. J., and F. L. Bookstein. 1987. A comment on shearing as a method for "size correction." Systematic Zool. 36:356–367.

Rojas, M. 1992. The species problem and conservation: what are we protecting? Conserv. Biol. 6:170–178.

Simpson, 1961. Principles of animal taxonomy. Columbia University Press, New York, NY.

Smith, M. F., and J. L. Patton. 1988. Subspecies of pocket gophers: causal bases for geographic differentiation of *Thomomys bottae*. Systematic Zool. 37:163–178.

Sullivan, R. M., and D. W. Nagorsen. 1998. *Tamias minimus* account. Pp. 54–55 *in* D. J. Hafner, E. Yensen, and G. L. Kirkland, eds. North American rodents: status survey and conservation action plan. IUCN Publications, Gland, Switz.

Yensen, E., and D. W. Nagorsen. 1998. *Thomomys talpoides* account. Pp. 66–67 *in* D. J. Hafner, E. Yensen, and G. L. Kirkland, eds. North American rodents: status survey and conservation action plan. IUCN Publications, Gland, Switz.