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Mystacina tuberculata.

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Mystacina Gray, 1843

Mystacina Gray, 1843:296. Type species *Mystacina tuberculata* Gray, 1843, by original designation (International Commission on Zoological Nomenclature [ICZN] 2002; Mayer et al. 1999).

Mystacops Lydekker, 1891:671. Unavailable replacement name for *Mystacina* Gray, 1843:296, proposed under the incorrect premise that *Mystacina* Gray is preoccupied by *Mystacinus* Boie, 1822 (Lydekker 1891; Mayer et al. 1999). *Mystacops* is on the Official Index of Rejected and Invalid Generic Names in Zoology (ICZN 2002).

CONTEXT AND CONTENT. Order Chiroptera, suborder Yangochiroptera (Teeling et al. 2005), superfamily Noctilionoidea (Kennedy et al. 1999; Kirsch et al. 1998; Pierson et al. 1986; Teeling et al. 2003; Van Den Bussche and Hoofer 2000), family Mystacinidae (Miller 1907). Genus *Mystacina* includes 1 extant species, *M. tuberculata*, and 1 recently extinct species, *M. robusta*, which has not been sighted since 1967 (Molloy 1995). *M. robusta* was originally described as a subspecies, *M. t. robusta* (Hill and Daniel 1985).

Mystacina tuberculata Gray, 1843

New Zealand Lesser Short-tailed Bat

Mystacina tuberculata Gray, 1843:296. Type locality "New Zealand;" and 1st use of current name combination.

Mystacina velutina Hutton, 1872:186. Type locality "[T]he Hutt Valley, near Wellington," North Island, New Zealand, and "Milford Sound, on the southwest coast of the South Island," New Zealand. This name is on the Official Index of Rejected and Invalid Specific Names in Zoology (ICZN 2002).

Mystacops tuberculatus: Lydekker, 1891:671. Name combination.

Mystacops velutinus: Thomas, 1905:423. Name combination.

CONTEXT AND CONTENT. Content as above. Three morphologically distinguished subspecies (Hill and Daniel 1985) are supported by some molecular data (Winnington 1999). Mitochondrial gene sequences distinguish 6 lineages (NW, NL, NE, S1, S2, and SN), with divergence dates of 0.93–0.68 million years ago (Lloyd 2003a). These lineages do not align with morphological subspecies listed below.

M. t. aupourica Hill and Daniel, 1985:294. Type locality "Omahuta Kauri Sanctuary, Northland, North Island, New Zealand, 35°10′S, 175°37′E."

M. t. rhyacobia Hill and Daniel, 1985:295. Type locality "Te Rimu area, upper Waimarino River, Kaimanawa Forest Park, SE of Lake Taupo, central North Island, New Zealand, 39°02′S, 175°56′E, ca. 700 ft."

M. t. tuberculata Gray, 1843:296; see above.

DIAGNOSIS. *Mystacina tuberculata* (Fig. 1) can be distinguished from the extinct *M. robusta* using the following measurements (range, in mm, *M. tuberculata* and *M. robusta*, respectively—Hill and Daniel 1985): length of forearm, 40.0–45 and 45.3–47.5; condylobasal length, 17.3–19.1 and 21.0–22.5; length of mandibular toothrow (c–m3), 7.3–8.0 and 8.9–9.4. Ears of *M. tuberculata* extend to, or beyond, tip of muzzle when laid forward; ears of *M. robusta* do not reach tip of muzzle when laid forward. Skeletal measurements distinguish the 2 species better than external features (Worthy and Scofield 2004).

Mystacina tuberculata is readily distinguished from *Chalinolobus tuberculatus*, the only other extant species of bat in New Zealand; *M. tuberculata* has pointed ears that extend past nose when laid forward, prominent tubular nostrils, and tail that extends 6–8 mm from dorsal surface of uropatagium, whereas *C. tuberculatus* has a tail fully enclosed in the uropatagium (Daniel 1990; Lloyd 2001).

Mystacina tuberculata and *C. tuberculatus* also can be distinguished by echolocation calls using a heterodyning bat detector. At 28 kHz, *M. tuberculata* echolocation flight calls are a series of short staccato clicks (20–50/s), whereas *C. tuberculatus* calls are a series of soft "thwacks" (8/s—Lloyd 2001).

GENERAL CHARACTERS. Pelage is very thick and velvety. Dorsal fur is grayish to dark brown and ventral fur is paler. Bare skin of ears, wings, nose, legs, and tail is gray-brown (Lloyd 2001). Unique external features of *M. tuberculata* include well-defined, thick, and striated proximal region of wing membranes and small basal talons at inside curve of toe and thumb claws.

Length of body is 60–70 mm plus ca. 20 mm with extended uropatagium; wingspan is 280–300 mm (Lloyd 2001). Tail reaches a length of up to 12 mm (Lloyd 2001) and projects 6–8 mm from uropatagium (Daniel 1990). Tibia is 14.5–17.0 mm in length and feet are stout, broad, and ca. 6 mm long (Lloyd 2001). Loose wrinkled skin covers soles of feet. Ears are 17.5–19.1 mm in length and 9 mm wide at base (Daniel 1990; Lloyd 2001). Tragus is simple, pointed, and ca. 10 mm in length (Lloyd 2001). Nostrils are large and vertically oblong. Muzzle is conical, obliquely truncated, relatively long, and has an array of whiskers encircling mouth and nostrils (Dwyer 1962a). Skull is twice as long as broad (Fig. 2), and width is ca. 1.33 times height of cranial cavity (Dwyer 1960a). Condylobasal length is 17.3–19.1 mm (sample size unknown—Hill and Daniel 1985).

Adults weigh 10–22 g before foraging (Lloyd 2001; O'Donnell et al. 1999). Body mass can increase by 20–30% while foraging, and preforaging body mass can increase by 20–30% during preparation for periods of torpor (Lloyd 2001). Female body mass can increase up to 35% during pregnancy (Lloyd 2001).

Morphometrics of *M. tuberculata* vary across subspecies and populations. Forearm measurements (mean, *SD*, and parenthetical range, in mm, sexes combined) are as follows: *M. t. aupourica* (*n* = 49): 40.90, 0.89 (36.95–42.00); *M. t. rhyacobia* (*n* = 999): 43.64, 1.24 (39.88–46.90); *M. t. tuberculata* (*n* = 304): 42.23, 1.01 (39.44–45.10—Lloyd 2001). Specimens of *M. tuberculata* from the Eglinton Valley of Fiordland had significantly greater

FIG. 1. Adult female *Mystacina tuberculata tuberculata* from the Eglinton Valley of Fiordland, New Zealand. Photograph by Daniel K. Riskin.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Mystacina tuberculata aupourica* collected at Omahuta Kauri Forest, New Zealand (Royal Ontario Museum specimen ROM80308). Greatest length of skull is 20.3 mm. Used with permission of the photographer J. L. Eger.

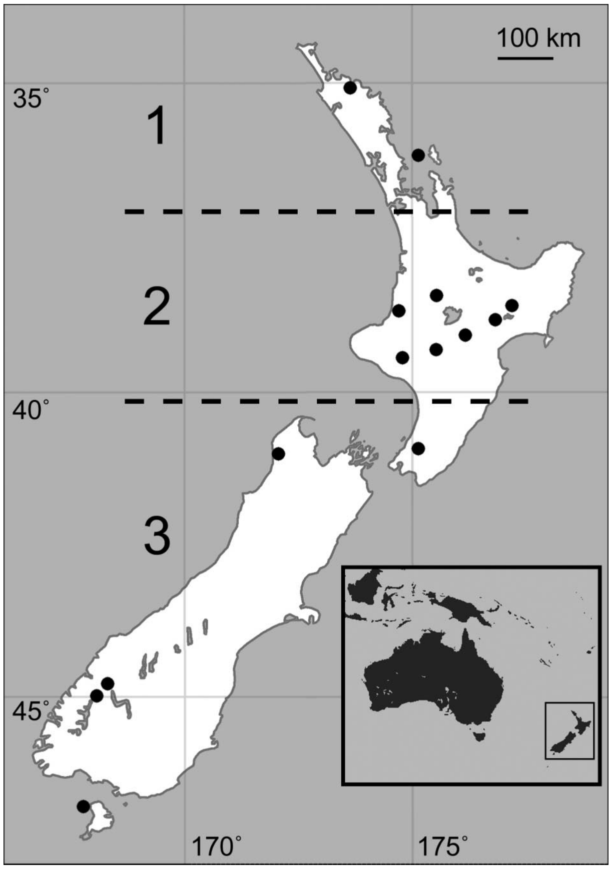

FIG. 3. Geographic distribution of populations of *Mystacina tuberculata* in New Zealand. Dots represent locations of known populations. Ranges of morphologically distinguished subspecies (1, *M. t. aupourica*; 2, *M. t. rhyacobia*; 3, *M. t. tuberculata*) are separated by dashed lines. Modified from the work of Lloyd (2003a; 2003b), with inclusion of a recently discovered colony at Dart Valley (C. F. O'Donnell, pers. comm.).

weights, larger forearms, and smaller ears, than those from Codfish Island and Little Barrier Island (O'Donnell et al. 1999). *M. tuberculata* in the Eglinton Valley is sexually dimorphic with respect to mass and forearm length, with females being significantly heavier and having longer forearms (O'Donnell et al. 1999). *M. tuberculata* on Little Barrier Island showed no difference in forearm length between males and females, although females were significantly heavier than males (Arkins 1996; Winnington 1999). *M. tuberculata* in Eglinton Valley also showed greater variation in size between age classes than did *M. tuberculata* on Codfish and Little Barrier Islands (O'Donnell et al. 1999).

DISTRIBUTION. *Mystacina tuberculata* is endemic to New Zealand (Fig. 3), where its distribution is highly correlated with presence of indigenous forest (Daniel and Williams 1984; Greaves 2005). On North Island, confirmed populations of *M. tuberculata* include a population at Omahuta-Puketi Forest in Northland, 7 large populations in central North Island, and a small genetically distinct population in the Tararua Ranges at the southern end of North Island (Lloyd 2001, 2003a). On South Island, isolated populations have been found in the Oparara Basin of Northwest Nelson, Eglinton Valley of Fiordland (O'Donnell et al. 1999), and Dart Valley of Aspiring National Park (C. F. O'Donnell, pers. comm.). Calls also have been recorded at Punakaiki on the West Coast (Lloyd 2001), and populations may exist in large unsurveyed forests of South Island (Greaves 2005). No calls have been recorded from surveyed forests around Mt. Taranaki, Wanganui River Trench, Matemateonga, Tongariro Forest, and the Ruahines (Lloyd 2001). Populations also exist on Little Barrier Island and Codfish Island, and a population is being established by the New Zealand Department of Conservation on Kapiti Island (B. D. Lloyd, in litt.). *M. tuberculata* is found from sea level to ca. 1,100 m, the highest altitudinal limits of New Zealand forest (Daniel and Williams 1984).

Six genetically distinguishable subspecies (Lloyd 2003a) are sympatric within most populations (Fig. 3) and correlate only roughly with distribution of 3 original morphologically based subspecies. Within central North Island, phylogeographical structure and demographic history of these 6 lineages of *M. tuberculata* is consistent with range expansion from scattered refugia following reforestation after catastrophic volcanic eruptions (Lloyd 2003b). On South Island, phylogeographical structure indicates a rapid southward expansion from refugia in northern South Island after postglacial reforestation of South Island 9,000–10,000 years ago (Lloyd 2003b).

FOSSIL RECORD. The fossil record provides strong evidence for an Australian origin for Mystacinidae. Fossilized teeth and dentary fragments from 3 species in the extinct mystacinid genus *Icarops* have been recovered in Australia (Hand et al. 1998). The fossils were found in freshwater limestone deposits at Bullock Creek (middle Miocene), Northern Territory, and Riversleigh (early Miocene Wayne's Wok site and Neville's Garden site), Queensland (Hand et al. 1998). Fossil materials of *Mystacina* from the late Quaternary have been collected from a series of New Zealand cave sites (Daniel 1990; Worthy and Holdaway 1994, 1995, 1996).

FORM AND FUNCTION. *Mystacina tuberculata* is capable of remarkable terrestrial and scansorial locomotion. Using hind limbs and wrists, they move quadrupedally on the ground. Up to the maximum observed speed of terrestrial locomotion (0.95 m/s), *M. tuberculata* used only 1 kinematically distinguishable gait, a symmetrical lateral-sequence walk that did not include an aerial phase. During terrestrial locomotion, the kinetic and potential energies of the center of mass did not change in a clear phase-locked fashion. Center of mass energetics were more runlike than walklike, and did not shift from walklike to runlike with increasing speed (Riskin et al., in press).

The external form and osteology (Dwyer 1960a, 1960b, 1962a) have unique characteristics relevant to terrestrial and arboreal locomotion. *M. tuberculata* can fold its wings within a protective sheathlike portion of wing membranes. A comprehensive description of wings and manner of wing folding (Dwyer 1962a) explains how fingers are enveloped within a thickened proximal region of propatagium, plagiopatagium, and uropatagium. Proximal phalanx of 3rd digit flexes inward beneath wing when folded, and distal phalanges are aligned with tibiae. A reduced propatagium facilitates greater mobility of forelimbs, and a reduced interfemoral membrane can be rolled proximally by calcars exposing only thickened portion of membrane. Robust pelvic girdle, hind limbs, and feet; a wide range of movement permitted by acetabulum; and basal talons on inside curve of claws and thumbs presumably aid in crawling and climbing (Dwyer 1960a, 1960b, 1962a). During terrestrial locomotion, the interfemoral membrane is raised by the calcar (W. Schutt, pers. comm.).

Mystacina tuberculata has distinctively thick fur and detailed accounts of hair structure exist (Dwyer 1960a, 1962a). Coarse overhairs are scattered among short and wavy underhairs. Diameter of hairs is irregular with typically 2 regions of swelling, near base and tip. Scale arrangement is annular, and scale form is appressed to divergent, entire to repand coronal (Dwyer 1960a, 1962a).

Mystacina tuberculata forages aerially in both cluttered and noncluttered environments, and also will commute considerable distances from roosting to foraging areas (Christie 2003b; O'Donnell et al. 1999); wing shape accommodates requirements of flight for these situations (Jones et al. 2003; Webb et al. 1998). A slightly low aspect ratio and low wing loading facilitate maneuverability, gleaning, and takeoff from the ground without sacrificing flight speed during commutes (Jones et al. 2003; Norberg and Rayner 1987). Other notable features of wings include a weak calcar extending from heel and 3 bony phalanges in 3rd digit (Dwyer 1960a, 1962a).

Mystacina tuberculata has basisphenoid pits for resonation with echolocation (Debaeremaeker and Fenton 2003). Strong premaxillae enclose small ventral palatal foramina and support large upper incisors (Dwyer 1960a). Even though *M. tuberculata* feeds on fruit and nectar in addition to insects, it has an essentially insectivorous dentition (Daniel 1976). Dental formula is i 1/1, c 1/1, p 2/2, m 3/3, total 28 (Daniel 1990). Lower incisors are closely crowded between canines and reduced in size, and tongue can be protruded over them through closed jaws (Daniel 1976). Vertebral formula is 7 C, 13 T, 5 L, 6 S, 8 Ca, total 39 (Dwyer 1960a). Seventh cervical and 1st thoracic vertebrae are fused (Dwyer 1960a). Sacral vertebrae are rigidly fused into sacrum, often along with posterior lumbar and 1st caudal vertebrae (Dwyer 1960a). Of 13 rib pairs, 9 are vertebrosternal, 2 are vertebrocostal, and 2 are vertebral (Dwyer 1960a). Scapula is robust, and secondary shoulder joint consists of an additional articular surface on dorsal and distal scapula (adjacent to supraglenoid tubercle) and an enlarged tuberculum majus (Schliemann 1997).

Tongue is adapted to nectivory; it is extensible, ca. 12 mm in length, ridged, and has a tip covered in hairlike papillae (Daniel 1976, 1979). One New Zealand lesser short-tailed bat had a nearly globular, thin-walled stomach and an intestine ca. 180 mm in length (Knox 1872).

ONTOGENY AND REPRODUCTION. *Mystacina tuberculata* has a long bicornuate uterus with considerable external fusion of cornua. Internally, separate lumina extend along most of length of uterine horns. Myometrial smooth muscle is present in wall of each cornua, where fused. Two specimens exhibited developing follicles in only right ovaries (Rasweiler and Badwaik 2000). Testes are internal throughout year (Lloyd 2001).

Mystacina tuberculata is monestrous with mating in summer and autumn followed by a delay in either fertilization, implantation, or development during winter (Daniel 1990; Lloyd 2001). Male singing begins in spring and early summer, from September to December, and courtship activity peaks during late summer and autumn, from February to May (Lloyd 2001). Vaginal plugs are present after mating (Lloyd 2001). Gestation begins or continues in spring and a single pup is born in summer (Daniel 1979, 1990; Krutzsch 2000). Parturition at ca. 35°S latitude occurs from December to January (Daniel 1990; Lloyd 2001). Within a single roost, births usually occur during a week-long period (Lloyd 2001).

No New Zealand lesser short-tailed bats caught ($n = 400$) during the winter on Codfish Island were pregnant, lactating, or postlactating, and adults and juveniles were indistinguishable (Sedgeley, in press; J. A. Sedgeley and M. Anderson, in litt.). During the summer, 2.8% were lactating females, 1.7% were postlactating, 11.8% were nonbreeding females, 21.1% were young of the year, and 62.6% were adult males ($n = 289$—Sedgeley, in press; J. A. Sedgeley and M. Anderson, in litt.). At Rangataua Forest in central North Island, ca. 80–90% of reproductively mature females breed each year, whereas 20% are reproductively immature (Lloyd 2001). On Little Barrier Island, 70% of female bats were pregnant or lactating in January (Winnington 1999).

At birth, young weigh ca. 5 g and have a forearm ca. 19 mm long; eyes are still closed 2 weeks after birth (Daniel 1979; Lloyd 2001). Bodies of neonates are hairless, deeply wrinkled, gray-black on dorsal surface, and pale grayish white on ventral surface (Daniel 1979; Lloyd 2001). Observations of a single offspring in captivity indicate that umbilical cord and placenta remain attached for 3 days; hind feet, legs, and claws are well developed at birth; ears remain stuck to sides of head for 5 days; and young are active and grooming after 1 day (Daniel 1979). After 3 weeks, milk teeth are replaced by permanent teeth and young begin exercising their wings. After 4 weeks, young are completely furred and flying (Lloyd 2001). At ca. 6 weeks, young leave the maternity roost and by 8–12 weeks are fully grown in skeletal size (Daniel 1990; Lloyd 2001). Postnatal development is rapid, with adult skeletal structure developing faster than adult mass (Arkins 1996; Daniel 1990).

ECOLOGY. Roosting and foraging normally take place in forest interiors. Large populations of *M. tuberculata* are restricted to extensive areas (>1,000 ha) of New Zealand's native forest that include many large trees suitable for colonial roosts, numerous epiphytes, and deep leaf litter (Lloyd 2001). New Zealand lesser short-tailed bats in the Eglinton Valley prefer roosting in forest stands with a relatively open structure (Sedgeley 2003).

Mystacina tuberculata will cross open grassland areas up to 2 km wide to reach foraging areas (O'Donnell et al. 1999), and small numbers have been recorded in scrubland, pine plantations, and farmland near old-growth forests (Lloyd 2001). On Codfish Island and Little Barrier Island, they have been observed foraging by cliffs and in grasslands (Arkins 1996; Daniel 1990; Winnington 1999).

Mystacina tuberculata has a diverse diet and flexible foraging strategy. In addition to insects and other small invertebrates, *M. tuberculata* ingests flower fragments, fruit, nectar, pollen, and wood (Arkins et al. 1999; Daniel 1976, 1979). *M. tuberculata* is an opportunistic forager whose diet corresponds with food abundance (Arkins 1996; Arkins et al. 1999). During a period of prolific fruiting, individuals fed almost exclusively on fruit of perching lily (*Collospermum microspermum*—Lloyd 2001). Fern and fungal spores occur on fur of *M. tuberculata* in Northland, including numerous spores of tree ferns (*Cyathea* and *Dicksonia squarrosa*) and an unidentified fungus, suggesting that *M. tuberculata* might also feed on them (Lloyd 2001). Historical reports suggested that *M. tuberculata* feeds on nestling birds and carrion (Stead 1936), but subsequent studies of diet of wild and captive bats do not support this suggestion (Arkins 1996; Arkins et al. 1999; Daniel 1976, 1979; Lloyd 2001; McCartney 1994). Captive individuals refused eggs, cheese, meat, and snails (McCartney 1994).

New Zealand lesser short-tailed bats are voracious foragers. One individual can consume in a day an amount of food equivalent to almost 50% of its body mass (Daniel 1979). In captivity, average nightly consumption was ca. 20 mealworms per individual (Daniel 1990), and an adult female bat weighing 20 g regularly consumed in addition to honey-water >9 g of moths over consecutive nights (Daniel 1979). Wild *M. tuberculata* individuals regularly consume

5–7 g of insects per night or 36–50% of prefeeding body mass (Lloyd and McQueen 2000).

No differences in diet were found among age and reproductive classes of New Zealand lesser short-tailed bats on Little Barrier Island (Arkins 1996). Relative abundances of taxa in fecal samples changed seasonally, but at all times 50% or more of diet consisted of the following insects: beetles (Coleoptera: Carabidae, Chrysomelidae, Curculionidae, and Scarabeidae), flies (Diptera: Chironomidae, Muscidae, Psychodidae, and Tipulidae), moths (Lepidoptera), and weta (Orthoptera—Arkins et al. 1999). Other consumed insects were from the orders Blattodea, Hemiptera, Hymenoptera (Formicidae), Neuroptera, Orthoptera (Rhaphidophoridae and Stenopelmatidae), and Thysanoptera (Terebrantia—Arkins et al. 1999). Other arthropods consumed by *M. tuberculata* included amphipods (Amphipoda), centipedes and millipedes (Myriapoda), harvestmen (Opiliones), mites (Acari), and spiders (Araneae—Arkins et al. 1999).

Fruits eaten by *M. tuberculata* include succulent bracts of kiekie (*Freycinetia bauriana*), berries of perching lilies (*Collospermum hastatum* and *C. microspermum*), and fleshy exocarp and mesocarp of hinau fruits (*Elaeocarpus dentatus*—Daniel 1979); additional fruits are also likely to be eaten (Daniel 1979; Lloyd 2001). Individuals in captivity have rejected fruits presented to them (McCartney 1994) or accepted apple, banana, feijoa, kiwi, peach, pepino, plum, and strawberry tree fruit (*Arbutus unendo*—Blanchard 1992).

Pollen from a wide variety of sources occurs in guano, stomachs, and fur of *M. tuberculata* from central North Island (Lloyd 2001), Little Barrier Island (Arkins 1996; Arkins et al. 1999), and Northland (Daniel 1976, 1979). *M. tuberculata* consumes pollen of perching lily (*C. hastatum*), rata and pohutukawa (*Metrosideros*), and rewarewa (*Knightia excelsa*) during their flowering periods (Daniel 1979; Lloyd 2001). In central North Island, the only commonly observed evidence of pollen feeding involved another perching lily (*C. microspermum*—Lloyd 2001). Pollen from kiekie (*Freycinetia baueriana*) and the endangered and endemic parasitic plant, wood rose (*Dactylanthus taylorii*) is found only occasionally (Lloyd 2001). Captive *M. tuberculata* ate a wide variety of native and nonnative flowers (Arkins et al. 1999; Blanchard 1992; McCartney 1994), but preferred nectar of *Eucalyptus*, variegata (*Metrosideros kermadecensis*), wood rose, and lobster claw (*Clianthus puniceus*), in that order (McCartney 1994). *M. tuberculata* will crawl over and tear apart *Astelia fragrans* and other flowers, and ingest the pollen from its body fur during subsequent grooming (Arkins et al. 1999; Blanchard 1992; Daniel 1979; Lloyd 2001).

Mystacina tuberculata pollinates a number of indigenous forest plants including kiekie, perching lilies (*C. hastatum* and *C. microspermum*), pohutukawa and rata (*Metrosideros*), and rewarewa (Lloyd 2001). *M. tuberculata* is an important pollinator of *D. taylorii*, New Zealand's only fully parasitic native angiosperm, and the only known ground-flowering plant to be pollinated by a bat (Ecroyd 1995). *M. tuberculata* also disperses seeds of New Zealand plants including kiekie and perching lilies (*C. hastatum* and *C. microspermum*—Daniel 1976; Lloyd 2001).

Until introduction of exotic mammals, *M. tuberculata* had no interactions with other terrestrial mammals. Unconfirmed evidence exists for predation, interspecific competition, and disturbance of nursery roosts by introduced mammals (Daniel 1990; Worthy 1997). Declines in *M. tuberculata* populations have been linked to introduction of the ship rat (*Rattus rattus*—Daniel 1990) and the much smaller kiore or Pacific rat (*R. exulans*—Worthy 1997). Both species of *Mystacina* disappeared from Big South Cape and Solomon Islands after introduction of *R. rattus* (Daniel 1990). Although high densities of *M. tuberculata* have coexisted with *R. exulans* on Little Barrier Island and Codfish Island (Lloyd 2001), increases in New Zealand lesser short-tailed bat populations occurred after eradication of *R. exulans* from Codfish Island (C. F. O'Donnell, pers. comm.). On central North Island, rats and other introduced mammalian predators have not had any obvious catastrophic effect on populations (Lloyd 2001).

Predators of *M. tuberculata* include the domestic cat (*Felis catus*), morepork (*Ninox novaeseelandiae*), New Zealand falcon (*Falco novaeseelandiae*), and extinct laughing owl (*Sceloglaux albifacies*—Dwyer 1960a, 1962a; Holdaway and Worthy 1996; Lloyd 2001). Of 22 mortalities, 6 were by cats and 1 by a morepork (Daniel and Williams 1984). Stoats (*Mustela erminea*) and rats (*Rattus*) have been observed at *M. tuberculata* roosts, but predation has not been confirmed (Lloyd 2001).

M. tuberculata host several unique species of parasites. *Chirophagoides mystacops*, described from one museum specimen of *M. tuberculata*, represents a new subfamily of mite (Daniel 1990; Fain 1963). A colony of 6 captive New Zealand lesser short-tailed bats died from infestation by the mite *Chirolaelaps mystacinae* (Heath et al. 1987a, 1987b). A 2nd species of *Chirolaelaps* mite occurs on *M. tuberculata* (Daniel 1990). Other mites include *Mystacobia hirsute* (Myobiidae) found in the fur (Uchikawa 1988), *Demodex mystacina* (Demodicidae) found in meibomian glands of eyes (Desch 1989), and *D. novazelandica* found in hair follicles near eyes (Desch 1989). *Mystacinobia zelandica* (Diptera: Mystacinobiae) is a large bat fly that feeds solely on guano (Holloway 1976). No nematodes or cestodes were found in 2 preserved specimens of *M. tuberculata* (Andrews and Daniel 1974), and no parasites were found in blood smears from 35 individuals from a colony in Omahuta (Daniel 1979). An opportunistic survey of disease in *M. tuberculata* from Codfish Island and Taranaki found no evidence of Australian bat lyssavirus and no significant bacterial pathogens, but did find a high prevalence of *Sarcocystis* (Protozoa) infection (20 of 55 individuals), the 1st report of *Sarcocystis* in bats (Duignan et al. 2003).

Prebreeding estimates of population size at Rangataua Forest over a 5-year period fluctuated between 5,740 and 6,977 (Lloyd 2001). Studies at other locations have reported minimum population estimates from 257 to 2,700 (Lloyd 2001; O'Donnell et al. 1999). Studies with marked individuals are difficult to conduct because forearm band markers injure wing and forearm of New Zealand lesser short-tailed bats (Lloyd 2001).

BEHAVIOR. During courtship, sexually active males occupy individual mating roosts in trees close to commuting paths or colonial roosts (M. J. Daniel and E. D. Pierson, in litt.; Lloyd 2001; O'Donnell et al. 1999). In Eglinton Valley, mating roosts were located in tree cavities 3.4–12 m above ground, and trees and cavities were generally smaller than those used for communal roosts (O'Donnell et al. 1999). Cavity entrances in Hall's totara (*Podocarpus hallii*) are polished with a brown oily secretion from throat glands of males (Lloyd 2001; C. F. O'Donnell, pers. comm.). This secretion has a distinctive musky smell and may attract females (Lloyd 2001). At night, males vocalize from mating roosts, calling for periods of 10–40 min at a time (O'Donnell et al. 1999). Mating calls are repetitive, audible to the human ear, and have a strong ultrasonic component (Lloyd 2001). Males will call in heavy rain and winds (Daniel 1990, in litt.). Females will fly 8–10 km to visit groups of calling males (Daniel 1990). Mating roosts are actively defended from other males and are used in subsequent years (M. J. Daniel, in litt.). In areas with less-predictable locations of female congregations, mating roosts near colonies are occupied only transiently (Lloyd 2001). Males audibly vocalize on what are presumed to be flyways (Winnington 1999).

Mystacina tuberculata has wide-bandwidth, multiharmonic echolocation calls with peak amplitude of 27–28 kHz (Jones et al. 2003; Parsons 2001). New Zealand lesser short-tailed bats also have brief, broad-band, frequency-modulated calls with steeply descending frequencies, a pulse repetition rate of 12.4–3.8 Hz, and a low duty cycle (Jones et al. 2003; Lloyd 2001; O'Donnell et al. 1999; Parsons 1997, 1998). Calls usually contain a fundamental and 2 other harmonics with an occasional 4th harmonic (Lloyd 2001; Parsons 2001). Frequency with the most energy is usually in the fundamental, but occasionally may be found in higher harmonics. Calls dominated by 1st harmonic sweep from 35.8 to 20.1 kHz. When 2nd harmonic is dominant, it sweeps from 60.6 to 41.9 kHz, and when 3rd harmonic is dominant, it sweeps from 92.6 to 66.8 kHz. Frequencies with the most energy averaged ca. 27, 48, and 76 kHz for 1st, 2nd, and 3rd harmonics, respectively (Parsons 2001). Calls have an average duration of 3.2 ms and an average bandwidth of 15.7 kHz (Parsons 2001). Calls and pulse intervals of New Zealand lesser short-tailed bats flying in forests are shorter than those released in open space away from trees (Jones et al. 2003). Lowest frequency and frequency of peak amplitude differed significantly between recordings from calls of New Zealand Lesser Short-tailed bats that were free-ranging, flying in a flight cage, or released from hand (Parsons 1998).

Automated monitoring systems (Arkins 1996; O'Donnell and Sedgeley 1994; Parsons 2001) are used to monitor *M. tuberculata*.

Each system has a bat detector, sound-triggered tape recorder, and a clock that announces the hour, and is used to detect *M. tuberculata*. In addition, an artificial neural network, trained and tested using power spectra of calls from *M. tuberculata*, can identify 100% of test calls to species (*n* = 92—Parsons 2001).

Mystacina tuberculata employs diverse behaviors when foraging for arthropods, including aerial pursuit, gleaning off vegetation and the ground, and digging through leaf litter (Blanchard 1992; Jones et al. 2003; Lloyd 2001; McCartney 1994). New Zealand lesser short-tailed bats are estimated to partition their foraging time as follows: 30% ground, foliage, and tree-trunk gleaning; 30% aerial insectivory; 20% frugivory; and 20% nectivory (Daniel 1976). Captive *M. tuberculata* spends ca. 40% of foraging time on the ground, 30% eating fruit or nectar, and 30% as an aerial insectivore (McCartney 1994). In terms of amount of time foraging on the ground, *M. tuberculata* is the most terrestrial bat.

In pursuit of nonflying prey, *M. tuberculata* uses echolocation, passive listening, and olfaction. Listening and olfaction are used to find prey buried under leaf litter or in crevices (Jones et al. 2003). *M. tuberculata* lands near prey and then pounces from the ground or disappears under leaf litter and reemerges sporadically (Jones et al. 2003).

Flight is often <2 m above the ground (Lloyd 2001). In mature beech and hardwood forests, *M. tuberculata* usually flies in the relatively open space between canopy and understory, but also can maneuver easily in restricted spaces (Christie 2003b; Lloyd 2001). Radiotagged New Zealand lesser short-tailed bats in central North Island and in southern South Island frequently commuted >10 km from their day roosts to forage (Lloyd 2001; O'Donnell et al. 1999). Mean flight speed is ca. 2.5 km/h, but individuals commuting long distances fly at speeds of up to 44.3 km/h (Christie 2003a, in press).

Home ranges of *M. tuberculata* near the southern extent of the species' range in the Eglinton Valley (Christie 2003a, in press; O'Donnell et al. 1999) are known. Four radiotagged *M. tuberculata* ranged over 130 km^2 spanning a 26.5-km length of the valley, with activity concentrated in a smaller core area (O'Donnell et al. 1999). Over 12 nights the home range of a single male averaged 16.0 km^2 (*SD* = 7.8 km^2, range, 10.4–25.0 km^2—O'Donnell et al. 1999). New Zealand lesser short-tailed bats (*n* = 21) ranged collectively over an area of 147 km^2, and most activity covered an area of 18 km^2 (Christie 2003a). Individual home ranges varied from 1.3 to 62.2 km^2 with a median of 4.8 km^2 (Christie 2003a).

Mystacina tuberculata depends almost exclusively on trees as roost sites, using cavities as communal and solitary roosts (Lloyd 2001; O'Donnell et al. 1999; Sedgeley 2003, in press). Communal roost sites are consistently larger than solitary roost sites with respect to size of cavity and tree diameter (Sedgeley, in press) and may contain up to 6,000 individuals (Lloyd 2001). New Zealand lesser short-tailed bats roosting communally show a higher degree of roost selectivity than those choosing solitary roosts (Sedgeley, in press). Communal roosts have less vegetative clutter in roost entrances, larger stem diameters at cavity height, greater cavity heights, and thicker cavity walls than other potentially available roosts (Sedgeley, in press). Roosts are generally selected in the oldest, largest trees of the forest, with larger than average stem diameters, a greater number of cavities, and stable internal temperatures (Sedgeley 2003, in press). Tree species preferred as roosts vary regionally and across forest types, and include kauri (*Agathis australis*) in mainland Northland, pohutukawa (*Metrosideros excelsa*) and puriri (*Vitex lucens*) in lowland forests of Little Barrier Island, matai (*Podocarpus spicatus*) in hardwood–podocarp forests, and red beech (*Nothofagus fusca*) and hard beech (*N. truncata*) in beech forests (Lloyd 2001). On Codfish Island, Hall's totara (*Podocarpus hallii*) was selected as a roost site more than would be expected if New Zealand lesser short-tailed bats chose roosts based on availability alone (Sedgeley, in press). Other tree species used as communal roosts include kahikatea (*P. dacrydioides*), kamahi (*Weinmannia racemosa*), rimu (*Dacrydium cupressinum*), silver beech (*N. menziessi*), southern rata (*M. umbellata*—Lloyd 2001), and miro (*Prumnopitys ferruginea*—C. F. O'Donnell, pers. comm.). Standing and fallen dead trees are occasionally used as roost sites (Daniel 1979; Sedgeley 2003).

Maternity roosts are occupied for 2–6 weeks (Lloyd 2001). Pups born outside maternity roosts are carried there soon after birth (Lloyd 2001). In the first 2 weeks after birth, lactating females roost with pups and return to feed them several times each night; later, females may stay in other communal roosts and only visit the maternity roost to feed young (Lloyd 2001). At this time, nonbreeding females and males may begin to use the maternity roost as a day roost (Lloyd 2001).

Although roosts selected in the summer versus the winter do not differ in structural and thermal characteristics (Sedgeley, in press), roosting behavior is variable seasonally, and regionally. Winter roosting behavior and activity at the southern extent of the species' range on Codfish Island are known (Sedgeley 2001). At this site, New Zealand lesser short-tailed bats selected among active communal roosts, relatively inactive communal roosts, and solitary roosts. Monitored communal roosts contained >100 individuals 75% of the time, with a maximum number of 1,443 counted at once (Sedgeley 2001). During winter in central North Island, *M. tuberculata* colonies are smaller than in summer, rarely containing >100–200 individuals, and are more stationary, remaining for up to several months in a single roost (Lloyd 2001). During the summer, *M. tuberculata* communal roosts in *Nothofagus* forest of Fiordland were dominated by females and young, with group size averaging 310 individuals (*SE* = 88.1 individuals, *n* = 40—Sedgeley 2003). New Zealand lesser short-tailed bats occupied the roosts for an average of 5.6 days (*SE* = 6.9 days, *n* = 23—Sedgeley 2003). Male and female *M. tuberculata* in Fiordland do not roost separately in sites with different characteristics during the reproductive season (Sedgeley 2003, in press).

Solitary *M. tuberculata* usually roost in small cavities in tree trunks, but individuals have roosted alone in large and otherwise empty communal roosts, under bark flakes, in small cavities in rotted wood, inside the trunk of dead tree ferns, at the base of perching lilies, and in holes in the ground (Lloyd 2001). During winter on Codfish Island, radiotagged *M. tuberculata* spent on average 57.1% of days (*SE* = 9.7%) in solitary roosts (Sedgeley 2001). In summer in southern South Island, radiotagged New Zealand lesser short-tailed bats used solitary roosts on 18.5% of radiotracking days (O'Donnell et al. 1999). The majority of solitary roosts on Codfish Island are used by nonbreeding New Zealand lesser short-tailed bats (Sedgeley, in press).

Mystacina tuberculata occasionally lives in crevices and burrows that they partially chewed out (Daniel 1979), and the unusually heavy wear observed on their incisors may be related to this unique behavior (Dwyer 1962b). At a colony of ca. 500 *M. tuberculata* roosting in a fallen giant kauri tree and at a similar roost 100 m away, cavities and tunnels had been chewed out (Daniel 1979). The wet floor of a particular roost was described as "honeycombed to a depth of about 1 m with tunnels and chambers excavated by the bats" (Daniel 1979:366). Signs of excavation included chewed wood mixed with bat guano and obvious tooth marks in both roosts. Cavities ca. 10 cm high by 8 cm wide and up to 50 cm deep were found with smaller tunnels several m long. In a 6 by 4-cm tunnel, New Zealand lesser short-tailed bats roosted in a line, oriented head to tail. By the time adult females and young had left the colony, entrance holes of tunnels had been enlarged more than twice in diameter. Maximum temperature taken over a 24-h period in 1 entrance hole was 39°C when individuals were active, and minimum temperature, recorded when individuals were inactive, was 15°C. Humidity was estimated to be 100% (Daniel 1979). Similar burrowing occurs in captivity (A. M. Arkins, in litt.). Colonies of *Mystacina* occur in abandoned sooty shearwater (*Puffinus griseus*) burrows and small holes in cliffs of volcanic pumice (Daniel 1979; Daniel and Williams 1984). No colonies have been found in caves in recent times, but large concentrations of mystacinid remains occur in caves (Daniel 1990; Lloyd 2001; Worthy and Holdaway 1994, 1995, 1996).

Mystacina tuberculata is often highly mobile among roosts. Individuals move between different occupied communal roosts and solitary roosts, staying at each for up to a few weeks at a time (Lloyd 2001; O'Donnell et al. 1999; Sedgeley 2003). Even in winter, large numbers of New Zealand lesser short-tailed bats move in and out of communal roosts, often simultaneously, throughout most of the night (Sedgeley 2001). Radiotagged New Zealand lesser short-tailed bats (*n* = 22) changed roost sites on average every 4.2 days (*SE* = 0.8 days) and moved between 35 different roosts over 38 nights (Sedgeley 2001). A roost tree occupied by several thousand New Zealand lesser short-tailed bats may be completely deserted the next day. Human or predator disturbance is a known stimulus for such movements (Lloyd 2001). Communal roosts can be used intermittently in this way for decades; a roost 1st found in 1932 on Codfish Island was still used in 1998 (Sedgeley 2003).

New Zealand lesser short-tailed bats visit communal night roosts that differ from their day roost. During winter on Codfish Island, up to 8 individuals visited a night roost simultaneously (Sedgeley 2001). Initiation of night roosting usually occurred 4–6 h after sunset and lasted on average 28.3% (*SE* = 3.8%) of the night with increasing lengths of night-roosting bouts correlated with decreasing nightly temperatures (Sedgeley 2001).

Nightly activity of *M. tuberculata* is highly variable. Observations of emergence time range from 21 to 150 min after sunset (Arkins 1996; Christie 2003a, in press; Daniel 1990; McCartney 1994; O'Donnell et al. 1999). Near the southern extent of range, nightly activity was characterized by an active period averaging 372 min (*SD* = 117.6 min; range, 210–530 min), a roosting spell of ca. 40 min (*SD* = 47.4 min; range, 10–110 min), and a 2nd active period of ca. 103 min (*SD* = 55.5 min; range, 60–180 min—O'Donnell et al. 1999). Another study in the same area found that New Zealand lesser short-tailed bats remained active throughout the night with only short and infrequent periods of inactivity ($\bar{X}$ = 16.1 min, *SD* = 7.8 min—Christie 2003a, in press). On Little Barrier Island, near the northern extent of range, activity around pohutukawa trees was smoothly unimodal, with peak activity occurring between 5 and 6 h after sunset (Winnington 1999). Activity patterns are typically unimodal on moonless nights, and although more variable on moonlit ones, are usually bimodal with 1 peak greater than the other (Arkins 1996). *M. tuberculata* is active in storm conditions (M. J. Daniel, in litt.; McCartney 1994).

Daily torpor is used by New Zealand lesser short-tailed bats in solitary roosts, but not at communal roosts (Sedgeley 2003). *M. tuberculata* uses extended torpor to conserve energy during cold periods (Lloyd 2001) and has a high frequency and long duration of winter activity and foraging, both inside and outside of roosts (Sedgeley 2001). *M. tuberculata* switches between solitary roosts, communal roosts of high activity, and communal roosts of low activity, and this ability to select winter roosts of varying activity levels may allow them to be active more frequently and for longer durations (Sedgeley 2001). Winter activity includes foraging, changing roost sites, social interaction, and possibly clustered thermoregulation (Sedgeley 2001). In central North Island, periods of torpor lasting up to 10 days are interrupted with periods of activity lasting from 1 h to several nights (Lloyd 2001). At the colder southern extent of its range on Codfish Island, *M. tuberculata* had high activity at low midwinter temperatures; a mean of 64.1% (*SE* = 6.5 %) of radiotagged individuals (*n* = 22) flew on monitored nights when mean minimum temperature was 3.4°C (*SE* = 0.5°C). On the coldest night (−1.0°C), 33% of radiotagged New Zealand lesser short-tailed bats remained active (Sedgeley 2001). *M. tuberculata* in the colder Eglinton Valley was encountered less frequently than on Codfish Island using automatic bat detector systems (Sedgeley 2001).

GENETICS. Karyotype of *M. tuberculata*, based on 1 adult female, has diploid number of 36 and fundamental number of 60 (Bickham et al. 1980) with 6 pairs of large chromosomes; 6 pairs of medium chromosomes; 2 pairs of small, biarmed chromosomes; and 4 pairs of small acrocentric chromosomes. Sex chromosomes were not characterized morphologically (Bickham et al. 1980).

CONSERVATION STATUS. *Mystacina tuberculata* is listed by the World Conservation Union (International Union for the Conservation of Nature and Natural Resources) as "vulnerable" (Hutson et al. 2001). *M. t. rhyacobia* is listed as a "range restricted" subspecies, whereas *M. t. aupourica* and *M. t. tuberculata* are listed as "nationally endangered" (Hitchmough 2002). Total population of *M. tuberculata* is estimated at ca. 50,000 individuals (Lloyd 2001, 2003b). Total estimate of major populations in the central and southern parts of North Island is <40,000; the most conservative estimate for those populations before humans arrived is 12.5 million (Lloyd 2003b). Because of a lack of evidence for adaptive divergence and the occurrence of sympatric phylogroups, *M. tuberculata* presents no easily defined, biologically meaningful, conservation units (Lloyd 2003b). Small and isolated populations at Omahuta, Tararua, Northwest Nelson, and Eglinton Valley were suggested for highest conservation priority by Lloyd (2003b).

Potential threats to *M. tuberculata* include habitat loss, invasive species, and poisons used in animal control (Hutson et al. 2001). *M. tuberculata* requires large areas of unmodified forest (Christie 2003a; Lloyd 2001; O'Donnell et al. 1999), and forest clearance and selective logging have dramatically reduced habitat (Molloy 1995). *M. tuberculata* poses challenges to conservation because of difficulty monitoring them and their concentration in large roosts (Lloyd 2001, 2003a). Secondary poisoning via arthropods that feed on 1080 poison baits is another threat; however, inspection of New Zealand lesser short-tailed bats (*n* = 269) after an aerial application of 1080 possum control baits did not find major mortality (Lloyd and McQueen 2002).

Mystacina tuberculata is protected under the Wildlife Act of 1953. A recovery plan was approved in 1995 and a national bat database has been established (Hutson et al. 2001). The New Zealand Department of Conservation is attempting to establish a new population on Kapiti Island by transferring 20 juveniles (B. D. Lloyd, in litt.).

REMARKS. The confusing nomenclatural history of *M. tuberculata* stems from the original description of the species by Gray in 1843 (Mayer et al. 1999). Because Gray believed only 1 bat species existed on New Zealand, his account is listed under the name *Vespertilio* (now *Chalinolobus*) *tuberculatus*, a species to which he gave authorship to "G. Forster," but after he examined 2 specimens he proposed the new genus *Mystacina*. Because Gray confused the 2 taxa and thus did not realize he had discovered a new species, the validity of *Mystacina tuberculata* Gray, 1843, has been debated. In Opinion 1994 of the International Commission on Zoological Nomenclature (2002), *Mystacina tuberculata* Gray, 1843, was conserved as the generic and specific name for this species. The generic name *Mystacina* comes from the Greek *mustax* meaning moustache, referring to the whiskers. The specific name *tuberculata* refers to small knobs on the upper lip of *C. tuberculatus* and was attributed to *M. tuberculata* because the 2 species were originally confused.

Mystacina has been placed in 7 different families and 4 superfamilies (Daniel 1990). Several studies (Kennedy et al. 1999; Kirsch et al. 1998; Pierson et al. 1986; Teeling et al. 2003, 2005; Van Den Bussche and Hoofer 2000) using a variety of molecular techniques provide robust support for *M. tuberculata* as a member of Noctilionoidea. The most recent 95% confidence interval of divergence time from other bats is 51–41 million years ago (Teeling et al. 2005).

The Maori term for bats is "peka peka." Variations on the common name include New Zealand New Zealand lesser short-tailed bat, lesser New Zealand lesser short-tailed bat, northern New Zealand lesser short-tailed bat, and New Zealand long-eared bat (Daniel 1990). Common names of subspecies are kauri forest New Zealand lesser short-tailed bat (*M. t. aupourica*), volcanic plateau New Zealand lesser short-tailed bat (*M. t. rhyacobia*), and southern New Zealand lesser short-tailed bat (*M. t. tuberculata*). The subspecific name of *M. t. aupourica* is derived from the Maori name Aupouri or Aupori for the northernmost peninsula of New Zealand (Hill and Daniel 1985). The subspecific name *M. t. rhyacobia* is derived from the Greek ρναξ, a stream of lava, and βιοσ, a manner of living, a reference to the area in which the specimen was found (Hill and Daniel 1985).

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