

A strange tale of taillessness in a vespertilionid bat

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INTRODUCTION

Having a well-developed tail and uroptagium is a key adaptation to aerial insectivory in bats (Lawlor, 1973; Bullen and McKenzie, 2001), with the exception of rhinopomatids (Schnitzler and Kallo, 2001), which have long tails, but reduced uroptagia (Nowak, 1994). I report on a little brown bat (*Myotis lucifugus*; Vespertilionidae) with an unusual morphology: the absence of a tail and a greatly reduced uroptagium. To my knowledge, this is the first record of taillessness in Vespertilionidae or in any aerial insectivores (M. B. Fenton, personal communication). I place my finding in two contexts: the defect's apparent effect on fitness and the potential evolutionary implications to the loss of the tail in certain phyllostomid lineages.

MATERIALS AND METHODS

I caught a tailless bat in the course of a three-year study of Prairie bats in southwestern Alberta, Canada, during which I captured a total of 2,125 bats, including 1,629 *M. lucifugus*, in mist nets erected in riparian sites on 160 nights. I took photos with a 35 mm digital camera (Canon PowerShot A560).

I backlit bats' wings, and classified bats with fused phalangeal epiphyses as adults and bats with visible cartilaginous gaps as juveniles (Anthony, 1988). I estimated the relative age of each adult by scoring canine tooth wear (Anthony, 1988), assigning it to one of seven classes (2 = youngest; canines no longer pinpoint sharp, 7 = oldest; well-worn canines). I scored bats with asymmetrical wear halfway between classes (e.g., 3.5 for a bat with right canine 3, left canine 4), and bats with one broken or missing canine according to wear on the intact tooth. I weighed each bat to the nearest 0.1 g on a digital balance, after holding it for at least an hour to allow it to void its digestive tract and provide an accurate mass. I measured forearm length to the nearest 0.1 mm with calipers. I estimated relative body condition following Entwistle *et al.* (1998) and Schulte-Hostedde *et al.* (2005) as the residual difference of individual mass from the expected value based on the within-group effect of forearm and date on mass ($r^2 = 0.20$, $F = 7.56$, $n = 65$, $P = 0.01$).

I visually examined males, classifying them as reproductive if they exhibited swelling of the caudae epididymides, where sperm are stored once spermatogenesis is complete (Entwistle *et al.*, 1998). Using calipers, I measured the linear extent of swelling to the nearest 0.1 mm along the craniocaudal axis, to assess the relative extent of spermatogenesis in reproductive males (P. A. Racey, personal communication). I calculated relative caudal swelling as the residual difference of individual caudal swelling from the expected value based on the within-group effect of body condition (the only significant predictor) on caudal swelling, excluding bats captured before the date on which I captured the first reproductive male ($r^2 = 0.09$, $F = 5.29$, $n = 55$, $P = 0.03$). To find information on vertebral formulae in various species of Phyllostomidae and on their primary modes of nutrition (Table 1), I conducted a literature search and consulted the National Science Foundation's Digital Morphology library, at www.DigiMorph.Org, which provides 3D digital images of the skeletons of certain bat species, taken by X-ray CT scan.

RESULTS

On 5.08.2008, at Fish Creek Provincial Park (50°55'38.14"N, 114°7'5.06"W), in Calgary, Alberta, Canada, I captured an adult male *M. lucifugus*. Although this bat had a severely reduced, symmetrically cleft-shaped uroptagium and no obvious caudal vertebrae, it had normal-looking calcars, a fringe of hairs on the trailing edge of the rudimentary membrane, no apparent scar tissue and showed no evidence of a past injury resulting in tail loss (Fig. 1).

The bat had a body mass of 6.7 g ($\bar{x} \pm SE = 8.0 \pm 0.23$ g, range 6.7–11.1 g; $n = 20$ adult male *M. lucifugus* captured on the same night), a forearm length of 37.4 mm ($\bar{x} = 38.0 \pm 0.06$ mm, range 35.0–40.6 mm; $n = 262$ adult male *M. lucifugus* over entire study), and exhibited slightly greater tooth wear (class 4) than the average adult male *M. lucifugus* over all three years of my study (class 3.7; $n = 248$). This bat was in below average body condition (Studentized residual -0.81; 95% LCI -0.25; UCI 0.25), with caudal swelling (5.1 mm) that was

TABLE 1. Numbers of caudal vertebrae and main food habits of phyllostomid bats

Taxon	Caudal vertebrae	Main food habit	Source
Subfamily Phyllostominae			
<i>Lonchorhina aurita</i>	8	Insectivory	Lassieur and Wilson (1989)
<i>Macrotus waterhousii</i>	7		Anderson (1969)
<i>Phyllostomus discolor</i>	7		Kwiecinski (2006)
<i>Vampyrum spectrum</i>	1–4, vestigial	Carnivory	Navarro and Wilson (1982)
Subfamily Glossophaginae			
<i>Anoura geoffroyi</i>	0–2	Nectarivory	Freeman (2000); Wetterer <i>et al.</i> (2000)
<i>Glossophaga moreno</i>	5		López González and Polaco (2001)
<i>Leptonycteris nivalis</i>	3		Pfimmer Hensley and Wilkins (1988)
<i>L. yerbabuenae</i>	3		Cole and Wilson (2006)
Subfamily Brachyphyllinae			
<i>Brachyphylla</i> spp.	3	Frugivory	Freeman (2000); Wetterer <i>et al.</i> (2000)
Subfamily Sturnirinae			
<i>Sturnira</i> spp.	0		Soriano and Molinari (1987)
Subfamily Stenoderminae			
	0		Wetterer <i>et al.</i> (2000)
Subfamily Carollinae			
<i>Carollia perspicilata</i>	4	Frugivory	DigiMorph.Org; Freeman (2000)
<i>Rhinophylla</i> spp.	0		Wetterer <i>et al.</i> (2000)
Subfamily Desmodontinae			
	0	Sanguivory	Greenhall <i>et al.</i> (1983); Wetterer <i>et al.</i> (2000)

below average (5.9 mm) but still within the 95% confidence interval (Studentized residual -0.15; 95% LCI -0.27; UCI 0.27).

DISCUSSION

That this is the first known report of taillessness in a vespertilionid bat speaks to the rarity of this defect, but the true rate at which it occurs is unknown, partly because reports of morphological abnormalities mainly come from field studies of volant bats rather than from forays into maternity colonies (but see Kunz and Chase, 1983).

As many bat species naturally lack tails and uropatagia, these features must not be critical to chiropteran success. However, in bats with well-developed tails and uropatagia (e.g., Vespertilionidae — Schutt and Simmons, 1998), they serve three functions. First, the uropatagium contributes to the total flight membrane surface area, generating lift and reducing wing-loading (Bullen and McKenzie, 2001), and the tail and uropatagium act as a rudder, allowing the bat to rotate and control pitch and yaw (Bullen and McKenzie, 2001). Second, foraging bats use them to scoop and direct insects toward the mouth (Webster and Griffin, 1962). Third, parturient

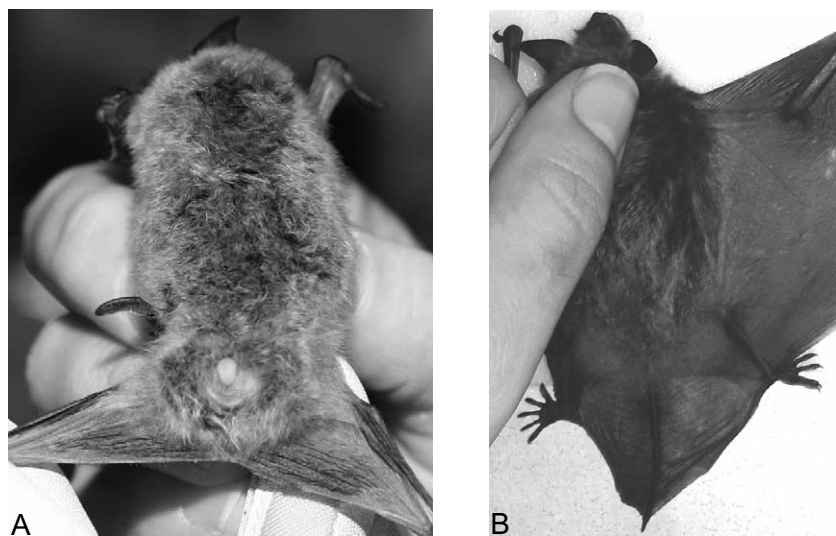


FIG. 1. Tailless (A) and morphologically normal (B) *M. lucifugus* captured on 5.08.2008 and 21.06.2006, respectively, in Calgary, Alberta, Canada

females deliver pups into a pouch formed by these structures (Wimsatt, 1960).

Myotis lucifugus, an aerial hawking/gleaning insectivore, uses its long tail (mean length: 37.4 mm — Van Zyll De Jong, 1985) and large uropatagium in all three ways above, and almost always in foraging (Wimsatt, 1960). Clearly, the problem of taillessness as it relates to parturition is not an issue for a male. However, by necessarily increasing wing-loading and stall speed, the defect should compromise the ability for slow flight and maneuverability, which should also be reduced by the lack of an effective rudder (Bullen and McKenzie, 2001). The lack of a scoop could also make prey capture more difficult and reduce the foraging success of a tailless *M. lucifugus* compared to a morphologically normal individual (Fig. 1B). Although these consequences of taillessness might be expected to add up to decreased fitness, several aspects regarding this individual suggest that its fitness was not severely compromised.

A key component of fitness is survival (Barclay and Harder, 2003), and first-year mortality in bats may be high, especially in temperate zones, where overwinter survival of juveniles is limited mainly by their ability to build up enough fat to fuel hibernation (Davis and Hitchcock, 1965). Not only was this bat an adult, but also it appeared slightly older than average, and had almost certainly overwintered more than once. The other major component of fitness is reproductive success (Barclay and Harder, 2003) and for bats, body condition is a key factor (Jakob *et al.*, 1996). In this respect, this bat was below average, but without knowing how much the tail and uropatagium contribute to a bat's total body mass, I cannot say what proportion of this difference is due to the mass of these lost structures. However, body condition also affects timing of spermatogenesis, another correlate of fitness (Entwistle *et al.*, 1998), and despite this bat's below average body condition, he had undergone spermatogenesis and was within the norm for caudal swelling.

This abnormality was apparently not due to injury, but rather was a congenital defect, given the lack of scars, the symmetry of the reduced uropatagium and the intact calcars and fringe of hairs normally present in some *Myotis* bats (Czech *et al.*, 2008). Although this defect could have resulted from damage sustained in utero, there is reason to suspect a genetic origin. Mutations causing taillessness are well-known in a number of domestic and laboratory mammals (Chesley and Dunn, 1936; Huston and Wearden, 1958; Todd, 1961; Indrebø

et al., 2008). In house mice (*Mus musculus*) and dogs (*Canis familiaris*), the mutation occurs at the T-locus (Dunn and Gluecksohn-Waelsch, 1953; Haworth *et al.*, 2001), and it may occur in the same locus in other tailless mutants, including bats (A. P. Russell, personal communication). Homozygosity for the mutation often causes severe spinal and urogenital abnormalities that hinder locomotion and reproduction, and may be lethal (Huston and Wearden, 1958; Haworth *et al.*, 2001). As DNA sampling was not part of my study protocol and as the *M. lucifugus* genome is not yet fully sequenced, I can only speculate that this bat was heterozygous for the tailless allele based on the lack of other major defects.

I noticed that the caudal area of this bat resembled the typical appearance of some phyllostomids, e.g., *Anoura geoffroyi*, *Artibeus jamaicensis*, and *Pygoderma bilabiatum* (photos at animaldiversity.ummz.umich.edu/site/accounts/classification/Phyllostomidae.html). Current knowledge of the processes that led to the diversification of bat tails and uropatagia is limited at least partly by an insufficient understanding of the genetic mechanisms that control their development (Tokita, 2006). Although we tend to think of evolution as a slow process, bats have undergone at least one rapid evolutionary change: digit elongation in ancestral Chiroptera — the result of a single locus mutation (up-regulation of Bmp2 growth factor — Sears *et al.*, 2006). Might a single locus mutation also be implicated in the rapid phenotypic divergence of phyllostomid tail morphology? Below, I provide support for this scenario.

First, primitive phyllostomids likely had tails and were mainly insectivorous, making taillessness and alternate food habits derived conditions (Freeman, 2000; Wetterer *et al.*, 2000). The only subfamily with genera (*Lonchorhina*, *Macrophyllum* and *Macrotus*) having long tails and well-developed uropatagia is Phyllostominae, which is also the only one that contains mainly insectivorous species (Freeman, 2000). Second, taillessness in Phyllostomidae seems to have arisen through heterochony, or reduction in the number of caudal vertebrae, as opposed to truncation, or reduction in vertebral length. Thus, compared to phyllostomines that are mainly insectivorous and have moderate to long tails, non-insectivorous phyllostomines and members of other phyllostomid subfamilies have fewer caudal vertebrae or none at all (see Table 1).

In conclusion, although taillessness might seem an insuperable obstacle to the success of an aerial insectivore, it does not seem to have reduced the

fitness of this individual. I also propose that the T-locus may be an appropriate starting point for investigating the genetic mechanism behind the evolutionary loss of the tail in the Phyllostomidae.

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