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Robust discrimination of *Reithrodontomys megalotis* and *R. montanus* (Mammalia: Rodentia) from Colorado, using cranial morphology and external characteristics within age classes

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Abstract.—*Reithrodontomys megalotis* and *R. montanus*, two species of harvest mouse that co-occur at low elevations of the southeastern Rockies and western Great Plains, are notoriously difficult to distinguish both externally and cranially, particularly for juveniles. Three external characteristics and 14 cranial measurements were used in discriminate function analyses (DFA) to detect the most robust measurements for species identification. Using 151 and 66 specimens of *R. megalotis* and *R. montanus*, respectively, from Colorado, we constructed DFA models for all specimens combined and segregated into four age classes by tooth wear. Due to substantial overlap in measurements, DFA models could not reliably predict species identity based on external or cranial characteristics alone, whereas models including all characteristics were more reliable. The most reliable DFA models were those for each age class (juvenile, subadult, adult, and old adult) using all external and cranial measurements. With various DFA models, 19 juvenile and subadult specimens of *Reithrodontomys* sp. from recent trapping efforts were all classified as *R. megalotis* with an average probability of 99.7%. Tail stripe width was also shown to be an unreliable identifier. We advocate using combined external and cranial measurements segregated by age class to robustly discriminate between these two species, particularly when identifying young individuals.

Keywords: Colorado, *Reithrodontomys*, rodent, skull morphology, species identification

Species are the fundamental units for assessments of biodiversity, ecology, evolution, and conservation (Wiens & Servedio 2000, Isaac et al. 2004, Rissler & Apodaca 2007). The necessity to correctly identify species is critical to robust scientific conclusions regardless of study question and vital for museum collections (Wilson & Reeder 2005, Christiansen 2008, Bitanyi et al. 2011, Gotzek et al. 2012). For well-known species like North American mammals, we assume that this is an error-free process but, for many small mammals, particularly shrews, voles, and some mice and bats, accurate species identifications necessitate cranial measurements, multivariate statistics, and DNA verification (Pocock & Jennings 2006, Nagorsen & Panter 2009, Fernandes et al. 2010, McGuire 2011, Thompson et al.

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2011). Two mice that are difficult to distinguish are *Reithrodontomys megalotis* and *R. montanus*, whose distributions overlap on the eastern side of the mountain states and the western-most plains states (Hall 1981, Linzey & Matson 2008, Linzey et al. 2008).

Both species are ecologically similar and occur in grasslands with some shrub cover (Webster & Jones 1982, Wilkins 1986). *Reithrodontomys megalotis* populations can occur at higher elevations (1050–1800 m) than *R. montanus* (1050–1500 m) in the foothills of Colorado (Armstrong 1972, Armstrong et al. 2011). The two species are currently distinguished in the field by overall size and differences in tail length and width of tail stripe: *R. megalotis* is bigger, with a longer tail bearing a wider stripe (Hoffmeister 1986, Armstrong et al. 2011). Because external characteristics are known to overlap substantially, cranial characteristics have been advocated for species identification (Hoffmeister 1986, Hoofer et al. 1999). Hoofer et al. (1999) used discriminant function analyses (DFA) of 11 cranial measurements to robustly distinguish the two species in Kansas. However, both Hoffmeister (1986) and Hoofer et al. (1999) only included adult or subadult specimens in their comparisons, either because they lacked young specimens or juvenile identifications were too problematic. Distinguishing juveniles and subadults can be critical for many studies since they are likely to be found at the dispersing edge of a population range, are often encountered in summer trapping after reproductive pulses, and are commonly caught in pitfall traps (Gaines & McClenaghan 1980, Johnson & Gaines 1988). Our initial tests applying Hoofer et al.'s (1999) DFA models with known specimens of *R. megalotis* from Colorado, including various age classes, detected high numbers of misclassifications (91%), but all *R. montanus* were correctly identified. This result implies that Colorado individuals differ in their cranial relationships or that models built solely with adults were poor predictors of identity across age classes. The latter is more likely since none of the adult *R. megalotis* were consistently misclassified using Hoofer et al.'s (1999) models.

In recent trapping efforts in the Colorado foothills, we collected 112 *Reithrodontomys* specimens of which more than half (74) were juveniles and subadults, and 19 lacked clearly identifiable external characteristics. Initially, several of these indeterminate specimens were assumed to be *R. montanus*, based on external characteristics and potential classifications from Hoofer et al.'s (1999) DFA models. One objective of our trapping study was to assess elevational range shifts in response to increased average annual temperatures (Moritz et al. 2008, Rowe & Lidgard 2009, Rowe et al. 2010). As global temperatures rise, *R. montanus* is predicted to expand its range upward elevationally, thus potentially overlapping more with *R. megalotis*. These 19 specimens tentatively identified as *R. montanus* would indicate an upward elevational shift of 200 m or more. We therefore focused on developing a robust DFA model to discriminate the two species in Colorado, including both juvenile and subadult age classes. With these models, we can compare the probability of the two species identification for the 19 *Reithrodontomys* sp. specimens and determine the necessity of DNA methods for reliable future identifications.

Materials and Methods

Specimens of *Reithrodontomys* used to build the discriminant function models are housed in the University of Colorado Museum of Natural History (UCM), including 46 *R. megalotis* and 5 *R. montanus* (Supplementary Materials: Appendix 1). These were supplemented by 105 specimens of *R. megalotis* from our recent collecting and 61 specimens of *R.*

montanus from other museums. In total, our Colorado sample of *Reithrodontomys* included 151 specimens of *R. megalotis*, 66 specimens of *R. montanus*, and the 19 specimens of *Reithrodontomys* sp. recently collected but of uncertain identity. Three external measurements provided by the collector (total length, tail length, hindfoot length) were included in the models. Ear length and body mass were excluded due to inadequate data coverage among specimens, particularly older specimens. Width of tail stripe on available, high-quality specimen skins (125 *R. megalotis*, 43 *R. montanus*) was designated as 'narrow' if the white underside of the tail could be seen either side of the stripe or 'wide' if not visible. Both fluid and stuffed specimens were examined, but excluded from the sample if the tail was broken or obviously altered due to the preparation method. Previous work recorded no strong sexual dimorphism in *Reithrodontomys* species (Webster & Jones 1982, Hoffmeister 1986, Wilkins 1986, Hoofer et al. 1999), as also corroborated by our data. *Reithrodontomys megalotis* had no significant size differences, except zygomatic plate and rostrum length (*t*-tests; $p = 0.01$, 0.01, respectively); *R. montanus* had no significant size differences, except rostrum breadth and interorbital breadth ($p = 0.01$, 0.02, respectively). Therefore, we do not include models specifically accounting for sexual dimorphism.

The 14 cranial characteristics measured were those examined in previous studies of *Reithrodontomys* (Hooper 1952, Hoffmeister 1986, Hoofer et al. 1999): skull length, zygomatic breadth, zygomatic plate breadth, braincase breadth, interorbital breadth, rostrum breadth (measured dorsal to the nasolachrymal capsules as in Hoofer et al. [1999]), rostrum length, nasal length, braincase depth, palate length, tooth row length, incisive foramen length, mesopterygoid fossa breadth, and breadth across occipital condyles. Each skull was assigned to one of four age classes based on tooth wear: juvenile = third molar erupting ($n = 34$); subadult = third molar in place with little to no wear ($n = 57$); adult = some wear on third molar ($n = 87$); old adult = molar cusps indistinct, dentine lakes broad ($n = 55$). SRBK measured all cranial measurements using Spi® digital calipers with 0.01 mm accuracy, using a magnifying glass as necessary. Measurement minima and maxima for the two species are given in Supplementary Materials (Appendix 2).

We assumed all specimens from existing collections were correctly identified to species, but to check for obvious outliers, we plotted each cranial characteristic individually against total length, skull length, and tail length among each species. One specimen was removed because five measurements were strong outliers, indicating an incorrectly identified *R. megalotis* (Utah Museum of Natural History [UMNH 27135], "*R. montanus*"). Another specimen that was a consistent outlier in model testing was removed, also indicating an incorrectly identified *R. megalotis* (University of Kansas [KU 68481], "*R. montanus*"). Many specimens were missing various external and cranial measurements, and the number of missing measurements increased within younger age classes (e.g., percentage missing values for *R. megalotis*: juvenile (86%), subadult (68%), adult (59%), and old adult (36%). Therefore, to increase sample sizes for specimens missing one or two measurements, we estimated the values based on the average from four specimens of the same species with the closest set of measurements (e.g., Horton & Kleinman 2007). Specimens with more than three missing variables were excluded from analyses (Supplementary Materials: Appendix 1), although they were used for models of unknown specimen identifications if the appropriate measurements were available for that model.

Discriminant function analyses (DFA) were conducted in JMP Pro 10 (SAS

Institute Inc. ©2012) for three datasets: the 'best' dataset with no estimated variables, the 'one estimate' dataset, and the 'two estimate' dataset (Table 1; Supplementary Materials: Appendix 3). Models were conducted using only external variables, only cranial measurements, and for all external and cranial measurements combined. Low log likelihood values (e.g., <1) and no misclassified specimens indicate strong DFA models. For strong models, we conducted stepwise DFA to detect the fewest variables necessary to clearly distinguish the two species. The age class DFA models included two datasets ('adult' = adult and old adult; 'juvenile' = subadult and juvenile) or included four datasets (old adult, adult, subadult and juvenile). These models were conducted for the three levels of data quality ('best,' 'one estimate,' 'two estimate') and the strongest of these models was conducted with stepwise variable selection to determine the fewest variables needed for a robust discrimination of species.

To obtain identifications of the 19 unknown *Reithrodontomys* specimens, the strongest possible DFA model was used to calculate the probability of species identification per specimen. Because all unidentified specimens were either juveniles (n = 11) or subadults (n = 8), all, except a single specimen, were missing some external or cranial variables. Therefore, an individual DFA model was constructed using all measurements available for that specimen and using all known specimens with that set of measurements. This increased sample size and strength of models (fewest misclassifications, lowest log likelihoods; Table 2). The subadult models were constructed with subadult specimens only, whereas for increased sample sizes of *R. montanus*, the models for juvenile identifications were constructed with subadult and juvenile specimens combined. No estimated values were used in specimen identification models.

Results

The discriminant function analysis (DFA) of the 'best' data set, including all external and skull variables detected no specimens as misclassified (n = 97, log likelihood = 5.64). Stepwise DFA identified nine variables necessary to robustly and correctly identify the two species (Fig. 1; 0 misclassifications, log likelihood = 6.53), including total length, tail length, hindfoot length, zygomatic breadth, zygomatic plate breadth, braincase breadth, interorbital breadth, rostrum breadth, and palate length. DFA models using only external characteristics or only cranial characteristics performed much worse (8 misclassifications, log likelihood = 34.72; 8 misclassifications, log likelihood = 42.76; respectively). DFA models with all variables included in the 'one estimate' and 'two estimate' datasets also performed worse than the model using 'best' data (n = 121, 4 misclassifications, log likelihood = 27.30; n = 152, 9 misclassifications, log likelihood = 46.34; respectively). Because the poor quality of estimated models indicates marginal value of estimated variables, estimates were not included in age class models. DFA models for two combined age classes, 'adults' and 'juveniles,' using all variables, performed better than the estimate datasets but still had one misclassification ('adults' = 69, 1 misclassified, log likelihood = 3.88; 'juveniles' = 19, 0 misclassified, log likelihood $<$ 0.0001).

DFA models for each of the four age classes had the strongest ability to discriminate between the two species, especially when using all variables (Table 1; 0 misclassifications, log likelihoods $<$ 0.0001 old adults, subadults, juveniles; 0 misclassifications, adults = 1.45). Stepwise DFA models by age class that resulted in no misclassifications included (Fig. 1): old adult (tail length, zygomatic plate breadth, and braincase breadth, log likelihood = 1.36); adult (12 variable model,

Table 1.—Discriminant function models to identify the strongest external and cranial measurements to discriminate between *Reithrodontomys megalotis* and *R. montanus* in Colorado. Datasets examined include: the best data with all variables measured (17), 1 estimate with all variables plus one missing variable estimated, 2 estimates with two missing values estimated, and age classes (combined juvenile and subadult, combined adult and old adult, juvenile, subadult, adult, old adult). DFA models were constructed for all variables, external variables, cranial variables, and a fewest variable model for strong models (no misclassifications, low log likelihood). Key to variables used: 1 = total length, 2 = tail length, 3 = hindfoot, 4 = skull length, 5 = zygomatic breadth, 6 = zygomatic plate breadth, 7 = braincase breadth, 8 = interorbital breadth, 9 = rostrum breadth, 10 = rostrum length, 11 = nasal length, 12 = braincase depth, 13 = palate length, 14 = toothrow length, 15 = incisive foramen length, 16 = mesopterygoid fossa breadth, 17 = occipital condyles breadth.

Model specimens	Model data	Model sample size	# Misclass.	Log-likelihood	# Variables (variables used)
Best	all variables	57, 30	0	5.64	17
	external only		8	34.72	3
	cranial only		8	42.76	14
	fewest variables		0	6.53	9 (1–3, 5, 7–9, 13)
1 Estimate	all variables	80, 41	4	27.30	17
	external only		14	64.94	3
	cranial only		17	67.49	14
2 Estimates	all variables	110, 42	9	46.34	17
	external only		18	96.78	3
	cranial only		18	87.77	14
Juv./Subadult	all variables	15, 4	0	<0.0001	17
	external only		1	2.87	3
	cranial only		0	<0.0001	14
	fewest variables		0	0.95	3 (8–9, 16)
Adult/Old adult	all variables	43, 26	1	3.88	17
	external only		7	28.84	3
	cranial only		5	28.24	14
	fewest variables		1	5.89	8 (1–2, 5–7, 9, 14, 16)
Juvenile	all variables	3, 1	0	<0.0001	17
	external only		0	<0.0001	3
	cranial only		0	<0.0001	14
	fewest variables		0	<0.0001	any 2 variables
Subadult	all variables	12, 3	0	<0.0001	17
	external only		0	0.02	3
	cranial only		0	<0.0001	14
	fewest variables		0	0.15	2 (1–2)
Adult	all variables	25, 13	0	1.45	17
	external only		5	23.27	3
	cranial only		3	14.82	14
	fewest variables		0	1.94	12 (2–3, 5–7, 9, 11, 13–17)
Old adult	all variables	18, 13	0	<0.0001	17
	external only		1	4.92	3
	cranial only		0	0.35	14
	fewest variables		0	1.36	3 (2, 6–7)

log likelihoods 1.94); subadult (total length and tail length, log likelihood = 0.15); juvenile (any two variables, log likelihood < 0.0001). Using cranial measurements alone, all age classes could be robustly discriminated to species, except for adults (Table 1). Three-variable, cranial DFA models without loss of discrimination could be determined for old adults (breadth of zygomatic plate, braincase breadth, and tooth row length), and subadults (skull length, braincase breadth, and mesopterygoid fossa breadth). Species could only be determined from external measurements alone with subadult specimens (Table 1).

Table 2.—Discriminant function models used to estimate the probability of a *R. megalotis* identification. For each juvenile specimen, the specimens from juvenile and subadult age classes were used; for subadults, only subadult specimens were used. Column details: Prob. of *R. megalotis* = probability of identification, Model sample size = the sample size for each species (*R. megalotis*, *R. montanus*) in the model, # Misclass. = number of misclassified known specimens, Log-likelih. = log-likelihood, # Variables = number of variables used in the model. Key to variables used: 1 = total length, 2 = tail length, 3 = hindfoot, 4 = skull length, 5 = zygomatic breadth, 6 = zygomatic plate breadth, 7 = braincase breadth, 8 = interorbital breadth, 9 = rostrum breadth, 10 = rostrum length, 11 = nasal length, 12 = braincase depth, 13 = palate length, 14 = toothrow length, 15 = incisive foramen length, 16 = mesopterygoid fossa breadth, 17 = occipital condyles breadth. Institution abbreviation: CMM = University of Colorado Museum of Natural History.

Specimen	Model age class	Prob. of *R. megalotis*	Model sample size	Model w/o specimen # Misclass.	Model w/o specimen Log-likelih.	# Variables (variables used)
CMM 649	juv/subadult	1.0000	17, 4	0	<0.0001	17 (1–17)
CMM 1244	juv/subadult	1.0000	22, 5	0	<0.0001	16 (1–4, 6–17)
CMM 468	juv/subadult	1.0000	17, 4	0	<0.0001	16 (1–3, 5–17)
CMM 1245	juv/subadult	1.0000	17, 4	0	<0.0001	16 (1–3, 5–17)
CMM 1243	juv/subadult	0.9998	17, 5	0	0.01	16 (1–3, 5–16)
CMM 480	juv/subadult	1.0000	18, 4	0	<0.0001	16 (1–15, 17)
CMM 618	juv/subadult	1.0000	19, 5	0	1.26	13 (1–3, 5–6, 8–11, 13–16)
CMM 650	juv/subadult	0.9985	37, 5	1	8.02	10 (2–3, 6, 8–11, 14–15, 17)
CMM 688	juv/subadult	0.9755	39, 6	4	15.99	10 (1–3, 6, 8–11, 14–15)
CMM 1114	juv/subadult	0.9992	50, 6	3	22.78	8 (1–3, 6, 8–9, 14–15)
CMM 654	juv/subadult	0.9925	50, 6	3	21.80	6 (1–3, 6, 8, 14)
CMM 646	subadult	1.0000	14, 3	0	<0.0001	16 (1–12, 14–17)
CMM 620	subadult	1.0000	19, 3	0	<0.0001	15 (1–12, 14–15, 16)
CMM 469	subadult	1.0000	16, 4	0	<0.0001	14 (1–4, 6–12, 14–16)
CMM 770	subadult	0.9995	20, 3	0	0.01	12 (1–3, 5–6, 8–11, 14–15, 17)
CMM 661	subadult	1.0000	23, 3	0	0.01	11 (1–3, 5–6, 8–11, 14–15)
CMM 539	subadult	0.9981	28, 4	0	0.92	10 (1–3, 6, 8–11, 14–15)
CMM 540	subadult	0.9961	27, 7	1	7.80	8 (6, 8–11, 13–15)
CMM 538	subadult	0.9820	31, 7	1	10.63	7 (6, 8–11, 14–15)

Model identifications of the unknown *Reithrodontomys* specimens were consistently *R. megalotis* for DFA models that included the measurements available for that specimen within its age class (Table 2). The average probability of an *R. megalotis* identification was 99.7% for unknown subadults and 99.7% for unknown juveniles. The two "*R. montanus*" specimens (UMNH 27135, KU 68481) that were identified as outliers and removed from analyses, were both re-identified as *R. megalotis* using the DFA old adult model ($p = 1$, log likelihood $= 0$), indicating misidentifications.

Width of tail stripe was only diagnostic of species identity if the tail stripe was thin (29 *R. montanus*, 1 *R. megalotis*), as wide stripes were present in both species (12 *R. montanus*, 142 *R. megalotis*). Thus, both models of external measurements and examinations of width of tail stripe indicate that species identifications are not always robust when based solely on external characteristics. The possible exception to this rule is subadults, although molar wear from a collected specimen is necessary for age determination.

Discussion and Conclusion

This study highlights the challenges of accurate species identification for understanding the ecology and distribution of a species (Wiens & Servedio 2000, Rissler & Apodaca 2007). Discriminant Function Analysis is a valuable tool for identifying

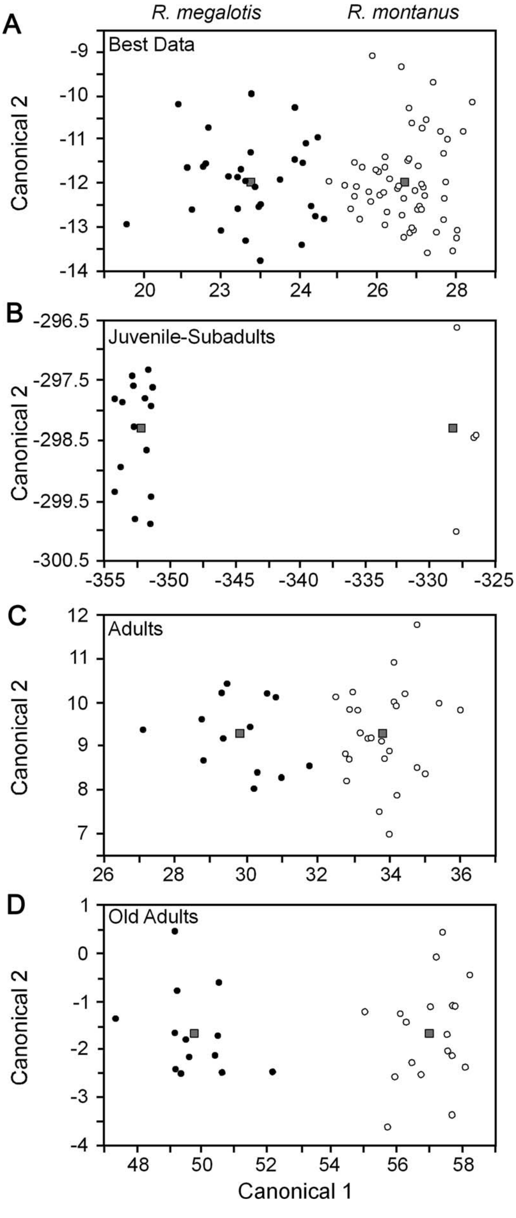

Fig. 1. Discriminant function analysis (DFA). A, 'best' data set including all external and skull variables; B, combined data of juveniles and subadults; C, adults; D, old adults. Data points shown for *Reithrodontomys megalotis* (black circles) and *R. montanus* (open circles), using stepwise DFA. Grey squares indicate centroid of each cluster.

species (Ruedi 1995, Hoofer et al. 1999, D'Anatro & Lessa 2006, Jansa et al. 2008, Bachanek & Postawa 2010, Conroy & Gupta 2011, Shahabi et al. 2011), and using this method, we were able to robustly differentiate between Colorado specimens of *Reithrodontomys megalotis* and *R. montanus* (Fig. 1). Our results concur with other studies finding the identification of these species problematic due to high overlap in measurements (Benson 1935, Hooper 1952, Hoofer et al. 1999). Previous field identifications were based on external measurements and tail morphology of the species (Armstrong 1972, Hoffmeister 1986, Armstrong et al. 2011), and although this has been carried out proficiently, our model shows that these measurements can be inadequate for species identification, particularly for younger individuals. Tail morphology, in particular, was used as an important species identifier (Armstrong et al. 2011); tail length is a critical variable in our DFA models, but the overlap in measurements makes it problematic when used alone. Tail stripe width also is not sufficiently diagnostic to be reliable, although the tail stripe morphology may be more diagnostic in live specimens than museum specimens.

Our models were most accurate at discriminating between the species when specimens were analyzed within age classes. This will not assist in field identification (e.g., mark and recapture) because a specimen is needed but allows collected specimens to be identified with statistical certainty without the need for DNA analyses. Compared to previous studies, we had a large sample size of old and young specimens on which to base our models (e.g., Hoofer et al. 1999: 6 old adults, 0 juveniles) leading to more robust identifications for young specimens. Proper species identification of juveniles is particularly critical, as this provides details of recruitment to the population, range expansions, and informs demographic analyses (Fisler 1971, Johnson & Gaines 1988, Reed & Slade 2007).

All biological science relies on the correct identification of species (Baker & Bradley 2006). *Reithrodontomys megalotis* and *R. montanus* are common and widespread species, sympatric through much of their range (Hill & Hibbard 1943). It is often assumed that more is known about common species than has actually been published (Gaston 2010). Yet, accurate identification of species is critical to their conservation (Barbosa et al. 2013), and the conservation of biodiversity in general (Isaac et al. 2004). In an era of anthropogenic climate change, it is of particular importance to be able to identify species at their range edges, to be able to track a population that may be critically contracting in range or declining in numbers. Range expansion was observed in *R. megalotis* in California (Moritz et al. 2008), so similar responses to climate change might be expected in other *Reithrodontomys* species. Using the DFA models to identify problematic juvenile specimens, we did not detect new *R. montanus* populations shifting westward and upward in elevation in the Colorado sites we sampled. Future researchers can also use these models and data (all specimen measurements are available upon request) to robustly identify new or existing specimens without the necessity of genetic analyses (Bradley et al. 2000, 2007; Gotzek et al. 2012).

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