

Demographical and morphological differences among coyotes (*Canis latrans*) relative to sampling method

Dave Shutler, Jenna M. Priest, Donald T. Stewart, and Michael Boudreau

Abstract: Collection methods can be biased, leading to misperceptions of population composition. We tested if collection method (footholds, snares, and shooting) gave different perceptions of demography or morphology of 3539 eastern coyotes (*Canis latrans* Say, 1823). We found no differences in sex ratios of animals among methods, but did find some evidence that younger, lighter, and smaller animals were more likely to be collected by footholds than with snares. Female reproductive histories (placental scars) did not differ among methods. In a subsample of 232 animals, we found no evidence of differences in helminth parasitism relative to collection method. Overall, our large sample for the non-parasite analyses facilitated finding statistical significance; the biological implications hinge on the precision required in estimating population composition and the focal characteristics being compared. For example, mass was 5.3% lower for coyotes caught with footholds versus snares and 10.4% lower for coyotes caught with footholds versus being shot, whereas linear trait measurements of coyotes caught with footholds were generally smaller by at most 4.5% compared with other methods (broadly consistent with linear versus volumetric measurements). Our study provides important baseline information for making inferences about populations of coyotes (and other species) sampled using only a single collection method.

Key words: *Canis latrans*, coyotes, capture bias, footholds, helminths, placental scars, snares.

Résumé : Des biais peuvent être associés à des méthodes de prélèvement, ce qui peut mener à des perceptions erronées de la composition de populations. Nous avons vérifié si différentes méthodes de prélèvement (pièges à patte, collets, armes à feu) produisent des perceptions différentes de la démographie ou de la morphologie de 3539 coyotes (*Canis latrans* Say, 1823). Nous n'avons relevé aucune différence du rapport de masculinité des animaux entre les méthodes, mais certaines données indiquent que les individus plus petits, légers et jeunes sont plus susceptibles d'être capturés dans des pièges à patte que dans des collets. Les antécédents de reproduction des femelles (cicatrices placentaires) ne varient pas d'une méthode à l'autre. Dans un sous-échantillon de 232 individus, nous n'avons relevé aucun indice de différence du parasitisme d'helminthes selon la méthode de prélèvement. Globalement, notre grand échantillon pour les analyses ne visant pas les parasites a facilité la détermination de la signification statistique; les conséquences sur le plan biologique dépendent de la précision requise pour l'estimation de la composition de la population et des caractéristiques qui sont comparées. À titre d'exemple, la masse est 5,3 % plus faible pour les coyotes capturés dans des pièges à patte que dans des collets et 10,4 % plus faible pour les coyotes capturés dans des pièges à patte qu'à l'arme à feu, alors que les mesures de caractère linéaires des coyotes capturés dans des pièges à patte sont généralement au plus 4,5 % inférieures par rapport aux autres méthodes (ce qui concorde grossièrement avec les différences entre les mesures linéaires et volumétriques). L'étude fournit d'importants renseignements de référence pour faire des inférences concernant les populations de coyotes (et d'autres espèces) en n'utilisant qu'une seule méthode de prélèvement. [Traduit par la Rédaction]

Mots-clés : *Canis latrans*, coyotes, biais de capture, pièges à patte, helminthes, cicatrices placentaires, collets.

Introduction

Unbiased samples of animals are commonly desired for numerous reasons, such as making inferences about populations (e.g., Pollock and Raveling 1982). However, it is generally impossible to know if a sample is unbiased (Burnham and Nichols 1985; Dufour et al. 1993a). A logical evaluation procedure is to use multiple sampling methods. If samples are similar in their composition, then one can be more confident that each method is unbiased. If samples are dissimilar, then one may be less confident in some or all sampling methods. Nonetheless, dis-

similarities may provide insight into the biology of one's study organism.

Biases in samples have long been recognized. For example, Bellrose (1959) found that lead-dosed waterfowl were more likely than undosed waterfowl to be among hunter-shot birds. Other studies have found age and sex biases in samples of collected animals (e.g., Chapman et al. 1969; Giroux and Bédard 1986; Buskirk and Lindstedt 1989; King et al. 2010), spatial variation in age and sex ratios (Ketterson and Nolan 1979), and personality differences in trapped animals (trap-happy vs. trap-shy; Nichols and Pollock 1983; Montiglio et al. 2012), to name a few. These and many

Received 20 July 2020. Accepted 13 November 2020.

D. Shutler and D.T. Stewart. Department of Biology, Acadia University, 15 University Avenue, Wolfville, NS B4P 2R6, Canada.

J.M. Priest. Department of Biology, Acadia University, 15 University Avenue, Wolfville, NS B4P 2R6, Canada; Nova Scotia Department of Lands and Forestry, Wildlife Division, Kentville, NS B4N 4E5, Canada.

M. Boudreau. Nova Scotia Department of Lands and Forestry, Wildlife Division, Kentville, NS B4N 4E5, Canada.

Corresponding author: Dave Shutler (email: dave.shutler@acadiau.ca).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from copyright.com.

other studies highlight ways that perceptions of the composition of populations may be flawed if collection biases are not recognized and controlled for (Dufour and Weatherhead 1991; Kerans et al. 1992; Senar et al. 1999a, 1999b; Cowan and Forrester 2012).

Various factors can contribute to biased samples. For example, some collection methods may be ineffective at certain times of year (e.g., birdsong playback may have limited success at attracting individuals outside the breeding season; Furness and Baillie 1981; Brotons 2000) or populations may have geographic variation in their composition, so that samples differ temporally or spatially (Herremans 1989; Slough and Mowat 1996; Whalen and Watts 1999). Another important source of bias in sampling is attractants (e.g., food, pheromones, playback). Weatherhead and Greenwood (1981) proposed the Condition Bias Hypothesis, which predicts that samples of animals attracted with food would be biased towards individuals in poorer condition. As a corollary to this, animals in poor condition may be less wary about artificial sources of food that may retain aversive human scent or other cues (Frank and Woodroffe 2001). Condition is generally deemed to be the amount of fat an animal carries relative to its body size (Green 2001; Schulte-Hostedde et al. 2005; Labocha and Hayes 2012). Condition is potentially influenced by several intertwined variables, including foraging ability, resource availability, and parasites. In any case, the Condition Bias Hypothesis has been tested and supported numerous times with multiple species (e.g., Borràs and Senar 1986; Dufour et al. 1993b; Gorney et al. 1999; Guyn and Clark 1999).

Weatherhead and Ankney (1984, 1985) subsequently suggested that not just food, but also social interactions, may attract waterfowl in poor condition. Therefore, a more general hypothesis, which we call the Collection Bias Hypothesis, considers a range of biases among samples collected in different ways that may be independent of condition (e.g., Cooch 1961; Greenwood et al. 1986; Figuerola and Gustamante 1995; Fast et al. 2008); the term capture bias is often used, but this would not apply to animals found dead (e.g., roadkill). All collection biases can have serious consequences for inferences about populations (Weatherhead and Ankney 1984; see also Burnham and Nichols 1985; Weatherhead and Ankney 1985). Regardless, knowing enough about one's study organism, one can make predictions about the direction of collection biases.

As part of a larger research program on eastern coyotes (*Canis latrans* Say, 1823) and an incentive program in Nova Scotia, Canada, a sufficient (>100) number of animals was collected using each of three different methods (footholds, neck snares (hereafter snares), and shooting), presenting an opportunity to evaluate if sample composition differed among collection methods. In Nova Scotia, footholds are invariably associated with some sort of attractant such as food or glandular lures; these are generally traps that have been modified to improve humaneness (M. Boudreau, personal observations) and meet the Agreement on International Humane Trap Standards (Government of Canada 2019). Snares are more likely to be deployed without attractants in areas perceived to have significant coyote traffic; we did not have data on whether snared coyotes were collected in association with attractants. Shot animals are collected in various ways; sometimes they are lured with calls, sometimes they are shot incidental to hunting for game species (such as deer and perhaps from a blind), and sometimes they are shot from a longer distance away in open areas while they are feeding on baits specifically used to attract coyotes and foxes (M. Boudreau, personal observations). Our predictions are based on the assumption that footholds more often rely on attraction by feeding than the other methods.

Based on the Condition Bias Hypothesis, we predicted that coyotes collected with footholds would be in poorer condition than animals collected with other methods. We also predicted that younger animals would be more likely to be collected by footholds than the other harvest methods because they would have greater nutritional demands for growth (McNab 1980), they would have less experience at recognizing potential threats associated with footholds, and they might be more willing to take bait due to inexperience at capturing food on their own. We were uncertain about sex biases in collection; at some times of year, females have high metabolic needs because of investment in offspring (Bronson 1985; Speakman 2008); however, at the same or different times of year, males can have high metabolic needs because of their larger size and because of costs of intrasexual selection (e.g., Moore and Millar 1986; Promislow 1992). Although the sexes differ in dispersal distances and timing (Hibler 1977; Patterson et al. 1999), we know of no clear reason that one collection method would be more likely to be biased in collecting a particular sex differently from the other methods.

Materials and methods

Study area

Nova Scotia, Canada (Fig. 1), is a peninsula surrounded by the Atlantic Ocean, connecting to New Brunswick, Canada, via an isthmus; habitat is described in Neily et al. (2017). Only 7% of the province is agricultural, whereas forestry is an important industry, so most forest in the province is successional. The province has Acadian, mixed, and boreal forest; some common tree species are white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and maple (genus *Acer* L.). Snowshoe hare (*Lepus americanus* Erxleben, 1777), white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), and Ring-necked Pheasants (*Phasianus colchicus* Linnaeus, 1758) are among the larger prey species available to coyotes.

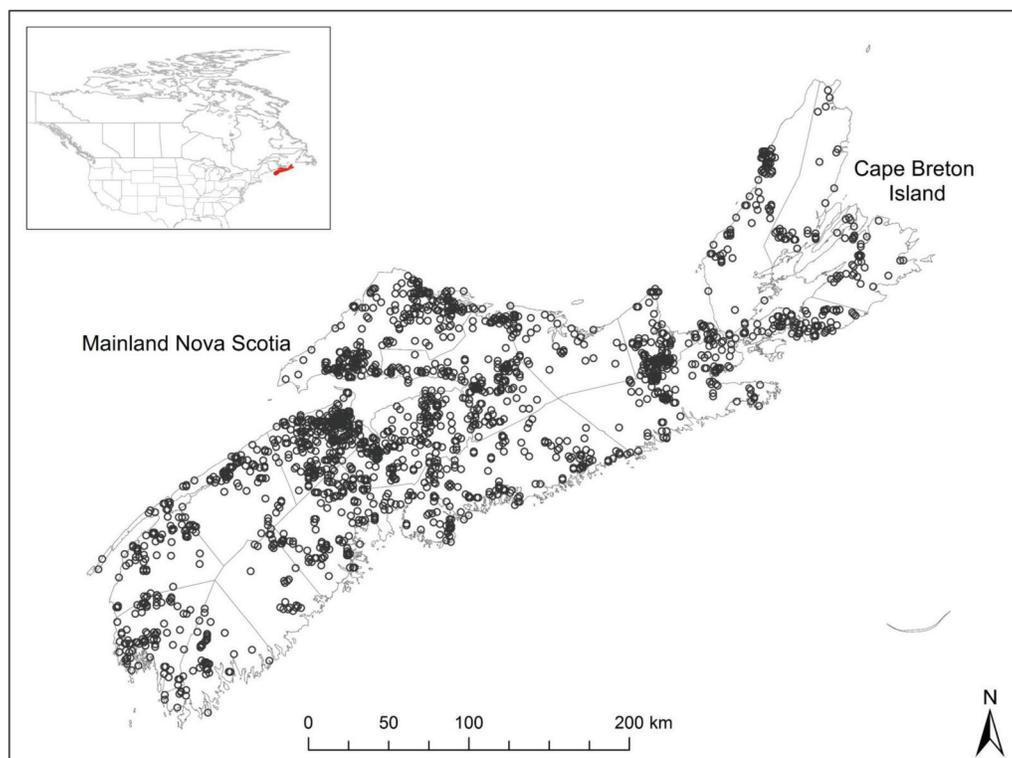
Collection, measurement, and sexing

Between September 2010 and March 2018, licenced trappers and hunters submitted carcasses to local provincial offices from throughout the province (Fig. 1); carcasses were transported to Kentville, Nova Scotia, for storage at -20°C prior to additional processing. According to guidelines (Canadian Council on Animal Care 2003), our research was exempt from review by an animal care committee because all tissues were sourced from animals harvested for non-research purposes. Of 4085 coyotes submitted to provincial offices, 3539 had at least some relevant data for at least one test. Most coyotes arrived skinned with information on date, location, and method of kill. Coyotes were thawed for 12–24 h at room temperature, weighed to the nearest 0.5 kg, and measured to the nearest centimetre for total body length (including the tail), chest width (by wrapping a measuring tape behind the scapula), and left shoulder length (measured from tip of the scapula to the base of the metacarpal pad). Coyotes were in most cases sexed based on external traits; in fewer than 5% of cases, sexing was confirmed using internal characteristics, with no conflicting assessments recorded.

Aging

As canids age, their tooth pulp cavity volume shrinks and the dentin becomes thicker. In the case of coyotes, subadults (i.e., ≤ 24 months old) have a ratio of pulp cavity width to total tooth width greater than 0.45 (Knowlton and Whittemore 2001). We removed lower jaws from carcasses and left them to simmer in a pot of water for 2 h at $\sim 95^{\circ}\text{C}$. Two canine teeth were extracted and X-rayed to quantify pulp cavity width. Digital calipers and a magnifying glass were used on X-rays to measure to the nearest

Fig. 1. Provenance of coyotes (*Canis latrans*) collected in Nova Scotia, Canada, from 2010 to 2018. Individual points may represent more than one animal. Map created using ArcGIS Desktop version 10.3.1 (ESRI, Inc., Redlands, California, USA) and assembled from the following data sources and shapefiles: Nova Scotia Department of Lands and Forestry GPS coordinates for harvested coyotes, Nova_Scotia_Counties (derived from Municipality shapefile downloaded from Geographic Data Directory; available from <https://nsgi.novascotia.ca/gdd/>), and Canada and US shapefiles (ESRI Software DVDs ArcMap version 8.0). Colour version online.



0.05 mm pulp cavity width and total tooth width, and animals were assigned to subadult or adult categories.

Condition

We first used a principal components (PC) analysis of total body length, tail length, chest width, and shoulder height (Supplementary Table S1).¹ The first PC explained more variation than expected by chance and all loadings were in the same direction, making PC1 a suitable measure of body size (Jackson 1993; Supplementary Table S1¹); remaining PCs explained less variation than expected by chance (Jackson 1993). Thus, in subsequent analyses we retained only PC1, designated SIZE. We then regressed mass against SIZE ($R^2 = 0.70$, $F_{[1,1660]} = 3867.4$, $P < 0.001$, with a very strong effect size of $\eta^2 = 0.70$; see below); residuals from this regression were used as indices of mass relative to body size (Schulte-Hostedde et al. 2005), designated CONDITION.

Helminth quantification

Beginning in 2017, we began helminth surveys on a subset of animals (results from earlier surveys reported in Power et al. 2015a). Details on methods are provided in Priest et al. (2018). Briefly, carcasses were thawed for 12–24 h, and trachea, heart, lungs, and intestinal tracts were flushed with tap water to collect helminths from organ lacunae. Tracheal surfaces were visually examined for nodules containing the nematode *Oslerus osleri* (Cobbold, 1879) (Polley 1986). Helminth data are being used primarily to monitor coyotes for parasites that may be transmitted to domestic dogs (*Canis familiaris* Linnaeus, 1758) and humans (Priest 2018; Priest et al. 2018).

Reproductive rates

Reproductive output from the previous year for female coyotes was determined by counting placental scars, which are dark, distinct patches in the uterine horns where developing embryos had been connected via a placenta to their mother (Davis and Emlen 1948; Gese et al. 1989). Reproductive tracts of female coyotes were removed, and an incision was made from the uterus to the ovaries, exposing the inner lining of the reproductive tract. Total number of placental scars reflects the maximum possible number of offspring produced by a female in the previous year (Todd and Keith 1983).

Analyses

All analyses were conducted in SAS version 9.4 (SAS Institute Inc., Cary, North Carolina, USA). Sample sizes differed among tests because some variables were not recorded for all animals. We tested for differences in categorical variables (sex, age, and parasite intensity and richness) using logistic regressions with collection method and day of the season as explanatory variables, and for differences in continuous variables (seven morphological metrics) with general linear models (GLMs). Because many females had no placental scars, we analyzed those data using Proc Genmod and a zero-inflated Poisson model. Confidence intervals (CIs) that we present are 95%, and all χ^2 values are Wald. As measures of effect sizes for GLMs, we computed η^2 (where 0.01 reflects a small effect size, 0.06 reflects a medium effect size, and 0.14 reflects a strong effect size) (Cohen 1988).

In Nova Scotia, seasons where footholds are legal extend from 15 October to 31 March, whereas for snares, seasons are from

¹Supplementary table is available with the article at <https://doi.org/10.1139/cjz-2020-0167>.

Table 1. Comparisons of numbers of each sex and age of coyotes (*Canis latrans*) collected by three different methods in Nova Scotia, Canada, from 2010 to 2018, and mean and standard deviation (SD) of date of collection, where 15 October = 1.

Age–sex group	Foothold			Snare			Shot		
	N	Mean date	SD	N	Mean date	SD	N	Mean date	SD
All data									
Subadult female	156	21.3	19.1	725	93.0	26.8	39	81.1	46.8
Subadult male	191	29.7	30.1	642	89.9	27.0	46	99.7	43.0
Adult female	131	27.9	25.7	624	94.1	27.0	48	105.0	44.3
Adult male	148	29.2	24.4	714	90.8	26.7	75	96.7	47.4
Overlapping dates									
Subadult female	39	47.6	18.3	689	90.8	24.0	28	81.4	34.1
Subadult male	63	62.9	30.6	611	88.9	23.7	30	93.5	24.5
Adult female	41	54.2	20.7	594	92.6	23.6	30	95.7	32.2
Adult male	54	53.1	24.6	683	89.8	23.4	46	88.7	31.3

Note: Refer to the text for the test statistics.

25 November to 28 February; shooting of coyotes is legal year round. To account for potential seasonal shifts in the metrics that we measured, we repeated analyses on data restricted to when collection dates overlapped. Moreover, in all analyses, we controlled for date of collection, where 15 October = 1 and 31 March = 167.

Results

Sample size, mean \pm standard deviation of collection data, and latest collection dates, respectively, were as follows: footholds 626, 11 November \pm 25.6, 23 March; snares 2705, 14 January \pm 26.8, 31 March; shot 208, 19 January \pm 46.0, 31 March. Data for only overlapping seasons were as follows: footholds 197, 9 December \pm 25.8, 29 February; snares 2577, 14 January \pm 23.6, 29 February; shot 134, 13 January \pm 30.8, 29 February.

Sex and age differences among collection methods

Of 3539 coyotes for which we had data, 1723 were female (48.7%; Table 1). Of 626 coyotes collected with footholds, 287 (45.8%) were female; of 2705 that were snared, 1349 (49.9%) were female; of 208 that were shot, 87 (41.8%) were female. Differences in sex ratios among methods were suggestive but not significant (Wald $\chi^2_{[2]} = 5.3$, $P = 0.07$); day of the season did not influence this result ($\chi^2_{[1]} = 1.8$, $P = 0.18$; overall model: $\chi^2_{[3]} = 9.2$, $P = 0.03$). Analyses restricted to overlapping collection dates yielded similar results (method: $\chi^2_{[2]} = 5.0$, $P = 0.08$; day of season: $\chi^2_{[1]} = 2.7$, $P = 0.10$; overall model: $\chi^2_{[3]} = 10.5$, $P = 0.01$).

With respect to age, 1799 (50.8%) coyotes in the sample were subadults (Table 1); subadults numbered 347 (55.4%) of animals collected with footholds, 1367 (50.5%) of those that were snared, and 85 (40.9%) of those that were shot. Differences in age ratios among methods were significant (Wald $\chi^2_{[2]} = 7.4$, $P = 0.03$); day of the season was not associated with a significant change in age structure ($\chi^2_{[1]} = 2.9$, $P = 0.09$; overall model: $\chi^2_{[3]} = 16.3$, $P = 0.001$). There were no significant associations when only coyotes from overlapping collection dates were analysed (method: $\chi^2_{[2]} = 2.6$, $P = 0.27$; day of season: $\chi^2_{[1]} = 1.1$, $P = 0.28$; overall model: $\chi^2_{[3]} = 3.9$, $P = 0.27$).

Morphological differences among collection methods

Five of seven morphological metrics (mass, chest, shoulder, SIZE, CONDITION) differed significantly among coyotes relative to collection methods, whereas body and tail length did not (Table 2); for simplicity, we present only results from overlapping collection dates; overall data produced generally similar

patterns). Overall, results suggested that animals were lighter, smaller, and in poorer condition when collected with footholds than with the other two methods, and there was a tendency for shot animals to be larger (Table 2), but with low effect sizes (Table 2). Within age–sex groups, there were fewer significant results (Fig. 2), but the pattern of foothold < snare < shot was broadly similar to the overall results.

Within animals only collected with footholds, those collected before 25 November were lighter and were smaller in chest and body length, but with low effect sizes (GLM: R^2 's ≥ 0.02 , F s ≥ 7.6 , P s ≤ 0.003 , $\eta^2 \geq 0.02$; tails and shoulder were not significantly different: R^2 's < 0.01 , F s ≤ 0.3 , P s ≥ 0.59 , $\eta^2 \leq 0.01$) than those collected after 25 November.

Reproductive and parasite differences among collection methods

We had data on placental scars for 858 subadults, of which 812 had no scars. All 151 subadult females collected with footholds had no placental scars; mean \pm 95% CI of scars were 0.2 ± 0.1 for 670 snared females and 0.2 ± 0.3 for 38 shot females (method: Wald $\chi^2_{[2]} < 0.1$, $P = 0.90$; day of season: $\chi^2_{[1]} < 0.1$, $P = 0.86$). Of 706 adult females, 444 had no scars. Mean \pm 95% CI of scars were 1.9 ± 0.5 for 117 females collected with footholds, 1.9 ± 0.2 for 560 snared females, and 1.3 ± 0.8 for 45 shot females (method: Wald $\chi^2_{[2]} = 0.3$, $P = 0.60$; day of season: $\chi^2_{[1]} = 1.1$, $P = 0.30$). Analyses restricted to data from overlapping collection dates led to similar conclusions.

More detailed parasite data are reported elsewhere (Priest 2018; Priest et al. 2018; J.M. Priest, D.L. McRuer, D.T. Stewart, M. Boudreau, J.W.B. Power, G. Conboy, E.J. Jenkins, and D. Shutler, unpublished data); briefly, we observed the lungworm nematode *Crenosoma vulpis* (Dujardin, 1845) (30% prevalence), lung nodule nematode *O. osleri* (33%), and intestinal tapeworm genus *Taenia* Linnaeus, 1758 (89%) at sufficient prevalences to test for differences in parasitism among collection methods; data for five other species with prevalences <14% were only used in computations of parasite diversity (i.e., number of species = richness). We found no significant differences in parasite metrics among collection methods (Table 3); *C. vulpis* prevalence declined significantly with day of the season ($\chi^2_{[1]} = 8.8$, $P = 0.003$), but day of the season was not associated with the other parasite metrics (all other $\chi^2_{[1]} < 0.8$, all other P s > 0.37). Analyses of data for only overlapping collection periods did not qualitatively change results for parasites.

Discussion

We found evidence that different collection methods provided different perceptions of the demographical and morphological

Table 2. Estimates from GLM tests for morphological differences among samples of coyotes (*Canis latrans*) collected with three different methods from Nova Scotia, Canada, from 2010 to 2018, using only data from times when all collection methods were being used.

Parameter	Mass	SE	Chest	SE	Body	SE	Tail	SE	Shoulder	SE	Size	SE	CONDITION	SE
N	2617		2465		2469		2352		1802		1678		1656	
Intercept	12.8	0.3	50.1	0.5	91.1	0.6	37.2	0.4	53.9	0.6	1.0	0.2	-0.7	0.2
Date	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1
Adult female	-0.5	0.1	0.1	0.2	-1.6	0.3	-1.5	0.2	-1.6	0.3	-0.6	0.1	0.3	0.1
Adult male	1.8	0.1	3.5	0.2	2.3	0.3	0.1	0.2	1.0	0.2	0.7	0.1	0.8	0.1
Juvenile female	-1.3	0.1	-1.8	0.2	-3.3	0.3	-1.5	0.2	-2.0	0.2	-1.1	0.1	0.0	0.1
Foothold	-1.1	0.3	-2.1	0.5	-0.8	0.6	-0.3	0.4	-2.1	0.6	-0.8	0.2	-0.2	0.2
Snare	-0.3	0.2	-1.3	0.4	0.1	0.5	-0.5	0.3	-1.6	0.4	-0.6	0.2	0.2	0.2
Model R ²	0.22		0.22		0.17		0.06		0.11		0.20		0.07	
Model F	126.0		113.1		81.7		25.9		37.4		70.6		21.2	
Date F	0.8		4.2		2.5		0.1		4.6		1.6		5.0	
Age-sex F	1213.6		216.2		160.7		50.0		67.3		134.3		34.0	
Method F	9.8		8.8		2.3		1.4		8.1		7.5		5.7	
Model P	<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001	
Date P	0.37		0.04		0.11		0.82		0.03		0.21		0.03	
Age-sex P	<0.001		<0.001		<0.001		<0.001		<0.001		<0.001		<0.001	
Method P	<0.001		<0.001		0.10		0.24		<0.001		<0.001		0.04	
Model η^2	0.22		0.22		0.17		0.06		0.11		0.20		0.07	
Date η^2	<0.01		<0.01		<0.01		<0.01		<0.01		<0.01		<0.01	
Age-sex η^2	0.22		0.21		0.16		0.06		0.10		0.19		0.06	
Method η^2	0.01		0.01		<0.01		<0.01		0.01		0.01		0.01	

Note: Data are further illustrated in Fig. 2. Models controlled for age-sex category as a class variable and day of the season (date, where 15 October = 1) on which animals were collected. SIZE is the first principal component (PC) from a PC analysis of chest, body length, tail length, and shoulder. CONDITION is residual mass from a regression of SIZE against mass. Foothold and snare estimates are relative to being shot, whereas the three age-sex category estimates are relative to juvenile males. Effect sizes (η^2) were medium to strong for overall models, small for methods, and medium to strong for age-sex categories.

composition of Nova Scotian coyote populations. The exception was for sex ratio (results were similar if we only analysed subadults or only adults). Most of our results suggested a slightly male-biased population in the province, consistent with Promislow (1992) who reported no sex bias in mortality for coyotes; in contrast, two congeners, gray wolves (*Canis lupus* Linnaeus, 1758) and golden jackals (*Canis aureus* Linnaeus, 1758), had slightly female-biased mortality. Trends for these latter two species are contrary to the overall pattern for mammals wherein species with larger males generally have male-biased mortality (Promislow 1992). In any case, the lack of sex differences among collection methods in our study suggests that any one method will give a reasonably good estimate of coyote population sex ratio.

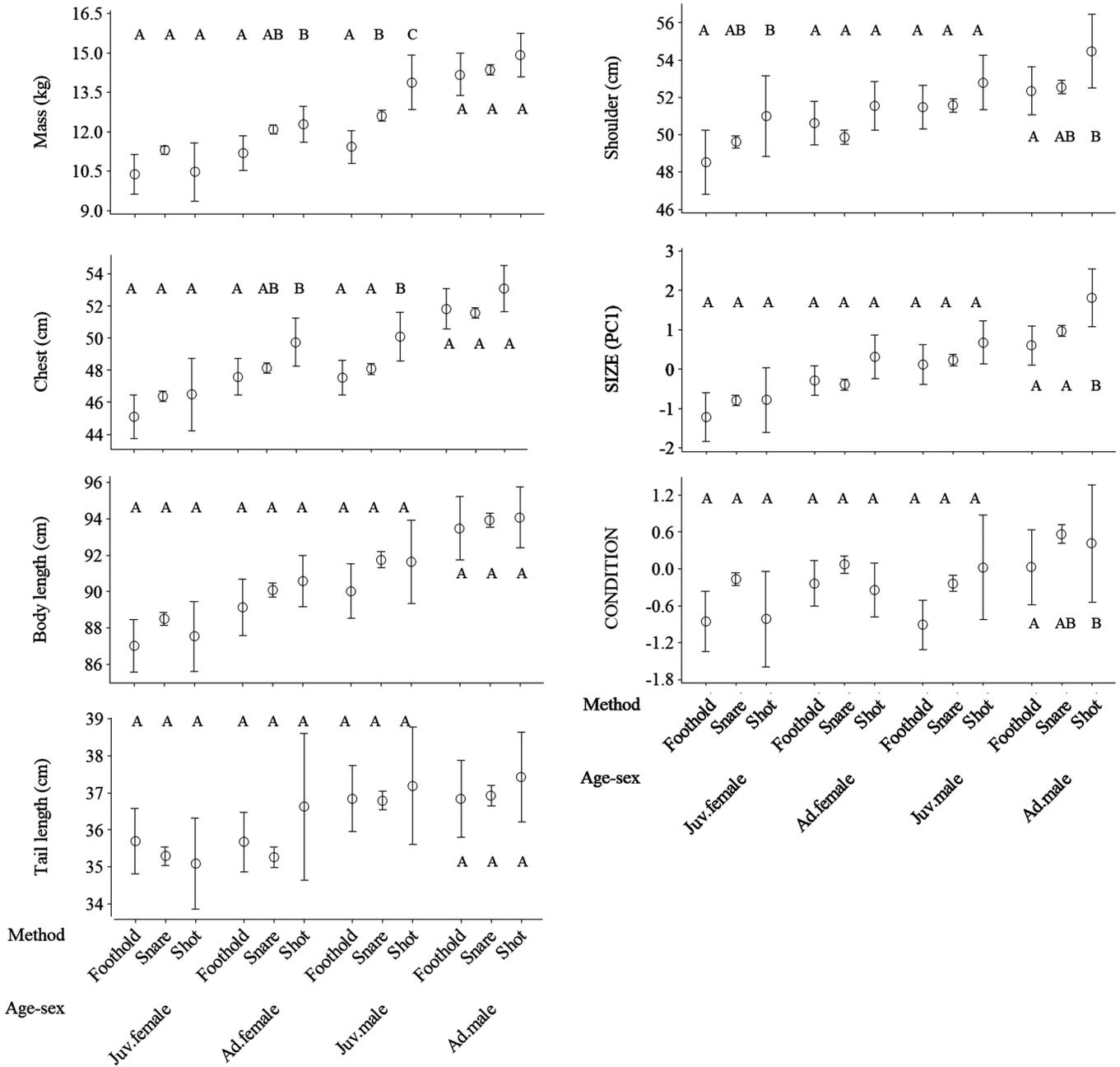
In contrast to our results for sex ratio, we found that younger, lighter, and smaller animals were collected more often with footholds than with the other collection methods. In general, these results support the Condition Bias Hypothesis (Weatherhead and Greenwood 1981). If so, then footholds may collect animals that are not as representative of the coyote population as are animals collected with snares or shooting. We deem it unlikely that larger animals would be more likely to escape footholds based on their design. The important point remains that the three sampling methods provided different pictures of the makeup of coyotes in Nova Scotia.

There is a long history of evidence for parasitized hosts being more susceptible to predation (Bethel and Holmes 1977; Hudson et al. 1992; McCurdy et al. 1999; Moore 2001), but we are aware of only one test that compared parasitism among animals collected by different methods: Temple (1987) found that prey captured by a trained Red-tailed Hawk (*Buteo jamaicensis* (Gmelin, 1788)) were more likely to be parasitized than were prey haphazardly collected by shooting. By definition, parasites harm their hosts. Harm may involve repair of tissue damage, energetic costs of mounting an immune response, or energy lost to the metabolic needs of the parasite (e.g., Shutler et al. 2012). Each of these investments could reduce host condition and render animals more susceptible to collection. To cause significant harm, para-

sites must often be sufficiently numerous and virulent (e.g., Gulland 1995; Tompkins et al. 1996); if effects are subtle, then large samples may be needed to detect effects (Booth et al. 1993; Shutler et al. 1999, 2012). Thus far, we have not detected significant effects of helminth parasites on measures of coyote health (J.M. Priest, unpublished data); accordingly, it may be no surprise that we observed no differences in parasitism among collection methods. However, samples are currently small for all but snared animals.

Biases among collection methods can occur for myriad reasons including spatial (e.g., Dufour et al. 1993a) and temporal (e.g., Greenwood et al. 1986) variation among populations. Moreover, we relied on submission of carcasses on a voluntary basis, and how carcasses were handled prior to submission was unknown. For example, significant variation in our data may have arisen because of the amount of time carcasses spent outside before being bagged and frozen, leading to significant variation in mass measurements. Additional variation could arise from variation in the percentage of genes coyotes retained from ancestral canid species (i.e., *C. latrans*, *C. lupus*, or *Canis lycaon* Schreber, 1775) (e.g., Power et al. 2015b; Heppenheimer et al. 2018). However, we have no reason to expect this variation would have been biased towards one collection method, and in general, such variation should have reduced our ability to detect collection biases. Despite this unmeasured variation, in our study, two key variables with significant biological importance, mass and CONDITION, were consistently lower for coyotes collected with footholds. Results for other morphological traits mostly told the same story, that animals collected in footholds were smaller. However, our large samples enabled us to obtain statistical significance despite small effect sizes, so the small *P* values that we obtained need to be considered in the context of their biological meaning. For instance, coyotes caught with footholds weighed 5.3% less than coyotes caught with snares and 10.4% less than coyotes that were shot, whereas linear traits of coyotes caught with footholds were generally smaller by at most 4.5% compared with other methods (broadly consistent with linear versus volumetric measurements).

Fig. 2. Interval plots (means and 95% confidence intervals) for seven morphological measures for four age–sex classes of coyotes (*Canis latrans*) collected from Nova Scotia, Canada, from 2010 to 2018. Subadults are animals <24 months old. Data are plotted separately for each of three collection methods; uppercase letters within age–sex classes that differ were statistically distinct. Also see Table 2.



One bias among collection methods in our study was that early in harvest seasons, coyotes were only collected with footholds before other methods were legal, and excluding these animals made differences in morphology among collection methods more subtle. Indeed, for just animals collected with footholds, those collected before 25 November were lighter and smaller than those collected later, likely because animals collected earlier had had less time to grow mature. Thus, restricting data to overlapping collection intervals provided a more robust test of collection bias.

Although collection bias has previously been reported for mammals (Buskirk and Lindstedt 1989; Tryjanowski et al. 2009;

Burger et al. 2009; Lapointe et al. 2015), the literature on this topic is mostly devoted to birds (Hepp et al. 1986; Heitmeyer et al. 1993; Vanderkist et al. 1999; Christensen 2001). Researchers need to be aware of potential misperceptions, as consequences of collection bias, of the makeup of their study populations. For Nova Scotia coyotes, our access to large samples enabled us to detect subtle differences among animals acquired with different collection methods; the importance of these differences will be context dependent. Although not a sure fix, having multiple sampling methods can increase confidence in estimates of population demography if each method gives similar results. However, multiple sampling methods incur greater costs and more hours to

Table 3. Number of coyotes (*Canis latrans*; sex and age classes pooled) infected with low or heavy intensities of common species of parasites, and total number of parasite species, relative to collection method (“other collection methods” pools footholds and shot) in Nova Scotia, Canada, from 2010 to 2018.

Parasite intensity or diversity	Snare	Other collection methods pooled	Odds ratio	Wald $\chi^2_{[1]}$	P
= 0 <i>Crenosoma vulpis</i>	152	13	1.97	1.0	0.31
>1 <i>C. vulpis</i>	55	4			
= 0 <i>Oslerus osleri</i>	144	14	1.92	1.0	0.33
>1 <i>O. osleri</i>	63	3			
<14 <i>Taenia</i> spp.	105	9	1.13	0.1	0.81
>14 <i>Taenia</i> spp.	102	8			
<2 species	121	13	2.45	2.2	0.14
>2 species	86	4			

Note: Shown also are statistics from logistic regressions where parasite intensity was the response variable and method and day of the season (15 October = 1) on which animals were collected (which was only significant for *C. vulpis*; Wald $\chi^2_{[1]} = 8.8$, $P = 0.003$; remaining: $\chi^2_{[1]} < 0.8$, $P_s > 0.37$) were explanatory variables. Odds ratios are the relative increase in the likelihood of having above median parasite metrics for snared animals.

collect and analyze data. In any case, if different sampling methods give different perspectives on a population, further scrutiny based on knowledge of the biology of one’s study organism may help pinpoint sources of bias, or suggest that new methods need to be used and evaluated. Regardless, blindly assuming knowledge of a population’s makeup based on any collection method entails risk, and where possible, this should be evaluated carefully. With respect to coyotes, footholds, snares, and shooting appear to provide similar information about population sex ratios, but footholds provide data suggesting lower ages and smaller sizes than data from snares and shooting. Nonetheless, it is impossible to know which method provides the more accurate representation of the population.

Acknowledgements

This study would not have been possible without the voluntary participation of members of the Trappers Association of Nova Scotia. Staff at offices of the Nova Scotia Department of Lands and Forestry, Wildlife Division, from across the province graciously collected and shipped carcasses, and numerous research assistants helped process carcasses and parasites. We thank F. MacKinnon for producing the map and A. Mullie for improving Fig. 2. We thank P. Cowan, L. Hayes, and D. Promislow for reprints and suggesting key references, and members of D. Shutler’s and D.T. Stewart’s laboratories for discussion and various forms of support. Funding was obtained from the Hunters and Trappers of Nova Scotia via the Nova Scotia Habitat Conservation Fund; the Nova Scotia Department of Lands and Forestry, Wildlife Division; a Natural Sciences and Engineering Research Council of Canada (NSERC) Undergraduate Research Award to J.M.P., and NSERC Discovery Grants to D.S. and D.T.S. We thank anonymous reviewers who provided many useful suggestions on the manuscript.

References

Bellrose, F.C. 1959. Lead poisoning as a mortality factor in waterfowl populations. *Illinois Nat. Hist. Surv. Bull.* **27**: 235–288. doi:10.21900/j.inhs.v27.172.

Bethel, W.M., and Holmes, J.C. 1977. Increased vulnerability of amphipods to predation owing to altered behaviour induced by larval acanthocephalans. *Can. J. Zool.* **55**(1): 110–115. doi:10.1139/z77-013. PMID:837268.

Booth, D.T., Clayton, D.H., and Block, B.A. 1993. Experimental demonstration of the energetic cost of parasitism in free-ranging hosts. *Proc. R. Soc. B Biol. Sci.* **253**: 125–129. doi:10.1098/rspb.1993.0091.

Borrás, A., and Senar, J.C. 1986. Sex, age and condition bias of decoy-trapped Citril Finches (*Serinus citrinella*). *Misc. Zool.* **10**: 403–406.

Bronson, F.H. 1985. Mammalian reproduction: an ecological perspective. *Biol. Reprod.* **32**: 1–26. doi:10.1095/biolreprod32.1.1. PMID:3882162.

Brotans, L. 2000. Attracting and capturing Coal Tits *Parus ater*: biases associated with the use of tape lures. *Ring. and Migr.* **20**: 129–133. doi:10.1080/03078698.2000.9674234.

Burger, J.R., Chesh, A.S., Castro, R.A., Tolhuysen, L.O., Torre, I., Ebensperger, L.A., and Hayes, L.D. 2009. The influence of trap type on evaluating population structure of the semifossorial and social rodent *Octodon degus*. *Acta Theriol.* **54**: 311–320. doi:10.4098/j.at.0001-7051.047.2008.

Burnham, K.P., and Nichols, J.D. 1985. On condition bias and band-recovery data from large-scale waterfowl banding programs. *Wildl. Soc. Bull.* **13**: 345–349.

Buskirk, S.W., and Lindstedt, S.L. 1989. Sex biases in trapped samples of Mustelidae. *J. Mammal.* **70**: 88–97. doi:10.2307/1381672.

Canadian Council on Animal Care. 2003. Guidelines on: the care and use of wildlife. Canadian Council on Animal Care, Ottawa, Ont.

Chapman, J.A., Henny, C.J., and Wight, H.M. 1969. The status, population dynamics, and harvest of the dusky Canada goose. *Wildl. Monogr.* **18**: 3–48.

Christensen, T.K. 2001. Effects of duckling body condition on hunting vulnerability in juvenile and immature common eiders *Somateria mollissima*. *Wildl. Biol.* **7**: 97–104. doi:10.2981/wlb.2001.013.

Cohen, J. 1988. Statistical power analysis for the behavioral sciences. Routledge, New York.

Cooch, G. 1961. Ecological aspects of the blue-snow goose complex. *Auk*, **78**: 72–89. doi:10.2307/4082236.

Cowan, P., and Forrester, G. 2012. Behavioural responses of brushtail possums to live trapping and implications for trap-catch correction. *Wildl. Res.* **39**: 343–349. doi:10.1071/WR11127.

Davis, D.E., and Emlen, J.T. 1948. The placental scar as a measure of fertility in rats. *J. Wildl. Manage.* **12**: 162–166. doi:10.2307/3796411.

Dufour, K.W., and Weatherhead, P.J. 1991. A test of the condition-bias hypothesis using Brown-headed Cowbirds trapped during the breeding season. *Can. J. Zool.* **69**(10): 2686–2692. doi:10.1139/z91-377.

Dufour, K.W., Ankney, C.D., and Weatherhead, P.J. 1993a. Nonrepresentative sampling during waterfowl banding: emphasis on body condition. *J. Wildl. Manage.* **57**: 741–751. doi:10.2307/3809074.

Dufour, K.W., Ankney, C.D., and Weatherhead, P.J. 1993b. Condition and vulnerability to hunting among mallards staging at Lake St. Clair, Ontario. *J. Wildl. Manage.* **57**: 209–215. doi:10.2307/3809415.

Fast, M., Clark, R.G., Brook, R.W., Fast, P.L., Devink, J.-M., and Leach, S.W. 2008. Eye colour, aging, and decoy trap bias in lesser scaup. *Can. Field-Nat.* **122**: 21–28. doi:10.22621/cfn.v122i1.538.

Figuerola, J., and Gustamante, L. 1995. Does use of a tape lure bias samples of Curlew Sandpipers captured with mist nets? *J. Field Ornithol.* **66**: 497–500.

Frank, L.G., and Woodroffe, R. 2001. Behaviour of carnivores in controlled and exploited populations. In *Carnivore conservation*. Edited by J.L. Gittleman, S.M. Funk, D.W. MacDonald, and R.K. Wayne. Cambridge University Press, Cambridge, U.K. pp. 419–442.

Furness, R.W., and Baillie, S.R. 1981. Factors affecting capture rate and biometrics of storm petrels on St Kilda. *Ring. and Migr.* **3**: 137–148. doi:10.1080/03078698.1981.9673772.

Gese, E.M., Rongstad, O.J., and Mytton, W.R. 1989. Population dynamics of coyotes in southeastern Colorado. *J. Wildl. Manage.* **53**: 174–181. doi:10.2307/3801326.

Giroux, J.F., and Bédard, J. 1986. Sex-specific hunting mortality of greater snow geese along firing lines in Quebec. *J. Wildl. Manage.* **50**: 416–419. doi:10.2307/3801097.

Gorney, E., Clark, W.S., and Yom-Tov, Y. 1999. A test of the condition-bias hypothesis yields different results for two species of sparrowhawks (*Accipiter*). *Wilson Bull.* **111**: 181–187.

- Government of Canada. 2019. Agreement on international humane trapping standards. Environment and Climate Change Canada, Gatineau, Que. Available from <https://www.canada.ca/en/environment-climate-change/corporate/international-affairs/partnerships-organizations/humane-trapping-standards.html> [accessed June 2019].
- Green, A.J. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology*, **82**: 1473–1483. doi:10.1890/0012-9658(2001)082[1473:MLRMOB]2.0.CO;2.
- Greenwood, H., Clark, R.G., and Weatherhead, P.J. 1986. Condition bias of hunter-shot mallards (*Anas platyrhynchos*). *Can. J. Zool.* **64**(3): 599–601. doi:10.1139/z86-088.
- Gulland, F.M.D. 1995. The impact of infectious diseases on wild animal populations: A review. In *Ecology of infectious diseases in natural populations*. Edited by B.T. Grenfell and A.P. Dobson. Cambridge University Press, Cambridge, U.K. pp. 20–51.
- Guyn, K.L., and Clark, R.G. 1999. Decoy trap bias and effects of markers on reproduction of Northern Pintails. *J. Field Ornithol.* **70**: 504–513.
- Heitmeyer, M.E., Fredrickson, L.H., and Humburg, D.D. 1993. Further evidence of biases associated with hunter-killed mallards. *J. Wildl. Manage.* **57**: 733–740. doi:10.2307/3809073.
- Hepp, G.R., Blohm, R.J., Reynolds, R.E., Hines, J.E., and Nichols, J.D. 1986. Physiological condition of autumn banded mallards and its relationship to hunting vulnerability. *J. Wildl. Manage.* **50**: 177–183. doi:10.2307/3801893.
- Heppenheimer, E., Cosio, D.S., Brzeski, K.E., Caudill, D., Van Why, K., Chamberlain, M.J., et al. 2018. Demographic history influences spatial patterns of genetic diversity in recently expanded coyote (*Canis latrans*) populations. *Heredity*, **120**: 183–195. doi:10.1038/s41437-017-0014-5. PMID: 29269931.
- Herremans, M. 1989. Habitat and sampling related bias in sex ratio of trapped Blackcaps *Sylvia atricapilla*. *Ringing Migr.* **10**: 31–34. doi:10.1080/03078698.1989.9676004.
- Hibler, S.J. 1977. Coyote movement patterns with emphasis on home range characteristics. M.Sc. thesis, Utah State University, Logan.
- Hudson, P.J., Dobson, A.P., and Newborn, D. 1992. Do parasites make prey vulnerable to predation? Red grouse and parasites. *J. Anim. Ecol.* **61**: 681–692. doi:10.2307/5623.
- Jackson, D.A. 1993. Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. *Ecology*, **74**: 2204–2214. doi:10.2307/1939574.
- Kerans, B.L., Karr, J.R., and Ahlstedt, S.A. 1992. Aquatic invertebrate assemblages: spatial and temporal differences among sampling protocols. *J. N. Am. Benthol. Soc.* **11**: 377–390. doi:10.2307/1467559.
- Ketterson, E.D., and Nolan, V., Jr. 1979. Seasonal, annual, and geographic variation in sex ratio of wintering populations of Dark-Eyed Juncos (*Junco hyemalis*). *Auk*, **96**: 532–536.
- King, D.T., Strickland, B.K., and Belant, J.L. 2010. Sex and age bias in American White Pelicans captured and collected on wintering grounds. *Waterbirds*, **33**: 546–549. doi:10.1675/063.033.0415.
- Knowlton, F.F., and Whitemore, S.L. 2001. Pulp cavity-tooth width ratios from known-age and wild-caught coyotes determined by radiography. *Wildl. Soc. Bull.* **29**: 239–244.
- Labocha, M.K., and Hayes, J.P. 2012. Morphometric indices of body condition in birds: a review. *J. Ornithol.* **153**: 1–22. doi:10.1007/s10336-011-0706-1.
- Lapointe, M.A., Bauer, C.M., Ebersperger, L.A., Reed, J.M., and Romero, L.M. 2015. Livetrapping is not biased by the endocrine stress response: a preliminary study in the degu (*Octodon degus*). *J. Mammal.* **96**: 762–771. doi:10.1093/jmammal/gyv081.
- McCurdy, D.G., Forbes, M.R., and Boates, J.S. 1999. Evidence that the parasitic nematode *Skrjabinoelava* manipulates host *Corophium* behavior to increase transmission to the sandpiper, *Calidris pusilla*. *Behav. Ecol.* **10**: 351–357. doi:10.1093/beheco/10.4.351.
- McNab, B.K. 1980. Food habits, energetics, and the population biology of mammals. *Am. Nat.* **116**: 106–124. doi:10.1086/283614.
- Montiglio, P.O., Garant, D., Pelletier, F., and Réale, D. 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, *Tamias striatus*. *Anim. Behav.* **84**: 1071–1079. doi:10.1016/j.anbehav.2012.08.010.
- Moore, G.C., and Millar, J.S. 1986. Food habits and average weights of a fall-winter sample of eastern coyotes, *Canis latrans*. *Can. Field-Nat.* **100**: 105–106.
- Moore, J. 2001. Parasites and behaviour of animals. Oxford Series in Ecology and Evolution. Oxford University Press, Oxford, U.K.
- Neily, P., Basquill, S., Quigley, E., and Keys, K. 2017. Ecological land classification for Nova Scotia. Nova Scotia Department of Natural Resources, Forestry Division, Truro, and Wildlife Division, Kentville.
- Nichols, J.D., and Pollock, K.H. 1983. Estimation methodology in contemporary small mammal capture–recapture studies. *J. Mammal.* **64**: 253–260. doi:10.2307/1380555.
- Patterson, B.R., Bondrup-Nielsen, S., and Messier, F. 1999. Activity patterns and daily movements of the eastern coyote, *Canis latrans*, in Nova Scotia. *Can. Field-Nat.* **113**: 251–257.
- Polley, L. 1986. Quantitative observations on populations of the lungworm *Oslerus osleri* (Cobbold 1889) in coyotes (*Canis latrans*). *Can. J. Zool.* **64**(10): 2384–2386. doi:10.1139/z86-354.
- Pollock, K.H., and Raveling, D.G. 1982. Assumptions of modern band-recovery models, with emphasis on heterogeneous survival rates. *J. Wildl. Manage.* **46**: 88–98. doi:10.2307/3808411.
- Power, J., Weatherbee-Martin, N., Boudreau, M., O'Brien, M., Conboy, G., and Smith, T. 2015a. Diversity and ecology of pulmonary metastrongyloidosis in coyotes (*Canis latrans*) of Nova Scotia, Canada. *Comp. Parasitol.* **82**: 85–93. doi:10.1654/4686.1.
- Power, J.W., LeBlanc, N., Bondrup-Nielsen, S., Boudreau, M., O'Brien, M., and Stewart, D.T. 2015b. Spatial genetic and body-size trends in Atlantic Canada *Canis latrans* (coyote) populations. *Northeast. Nat.* **22**: 598–612. doi:10.1656/045.022.0314.
- Priest, J.M. 2018. Host–parasite associations in coyotes (*Canis latrans*). B.Sc. Honours thesis, Acadia University, Wolfville, N.S.
- Priest, J.M., Stewart, D.T., Boudreau, M., Power, J., and Shutler, D. 2018. First report of *Angiostrongylus vasorum* in coyotes in mainland North America. *Vet. Rec.* **183**: 747–747. doi:10.1136/vr.105097. PMID:30514743.
- Promislow, D.E.L. 1992. Costs of sexual selection in natural populations of mammals. *Proc. R. Soc. B Biol. Sci.* **247**: 203–210. doi:10.1098/rspb.1992.0030.
- Schulte-Hostedde, A.I., Zinner, B., Millar, J.S., and Hickling, G.J. 2005. Restitution of mass–size residuals: validating body condition indices. *Ecology*, **86**: 155–163. doi:10.1890/04-0232.
- Senar, J.C., Conroy, M.J., Carrascal, L.M., Domènech, J., Mozetich, I., and Uribe, F. 1999a. Identifying sources of heterogeneity in capture probabilities: an example using the Great Tit *Parus major*. *Bird Study*, **46**: S248–S252. doi:10.1080/00063659909477251.
- Senar, J.C., Domènech, J., and Conroy, M.J. 1999b. Funnel traps capture a higher proportion of juvenile Great Tits *Parus major* than automatic traps. *Ringing Migr.* **19**: 257–259. doi:10.1080/03078698.1999.9674189.
- Shutler, D., Alisauskas, R.T., and McLaughlin, J.D. 1999. Mass dynamics of the spleen and other organs in geese: measures of immune relationships to helminths? *Can. J. Zool.* **77**(3): 351–359. doi:10.1139/z98-226.
- Shutler, D., Alisauskas, R.T., and McLaughlin, J.D. 2012. Associations between body composition and helminths of lesser snow geese during winter and spring migration. *Int. J. Parasitol.* **42**: 755–760. doi:10.1016/j.ijpara.2012.05.008.
- Slough, B.G., and Mowat, G. 1996. Lynx population dynamics in an untrapped refugium. *J. Wildl. Manage.* **60**: 946–961. doi:10.2307/3802397.
- Speakman, J.R. 2008. The physiological costs of reproduction in small mammals. *Philos. Trans. R. Soc. B Biol. Sci.* **363**: 375–398. doi:10.1098/rstb.2007.2145. PMID:17686735.
- Temple, S.A. 1987. Do predators always capture substandard individuals disproportionately from prey populations? *Ecology*, **68**: 669–674. doi:10.2307/1938472.
- Todd, A.W., and Keith, L.B. 1983. Coyote demography during a snowshoe hare decline in Alberta. *J. Wildl. Manage.* **47**: 394–404. doi:10.2307/3808512.
- Tompkins, D.M., Jones, T., and Clayton, D.H. 1996. Effect of vertically transmitted ectoparasites on the reproductive success of swifts (*Apus apus*). *Funct. Ecol.* **10**: 733–740. doi:10.2307/2390508.
- Tryjanowski, P., Sparks, T.H., Kamieniarsz, R., and Panek, M. 2009. The relationship between hunting methods and sex, age and body weight in a non-trophy animal, the red fox. *Wildl. Res.* **36**: 106–109. doi:10.1071/WR08036.
- Vanderkist, B.A., Xue, X.H., Griffiths, R., Martin, K., Beauchamp, W., and Williams, T.D. 1999. Evidence of male-bias in capture samples of Marbled Murrelets from genetic studies in British Columbia. *Condor*, **101**: 398–402. doi:10.2307/1370004.
- Weatherhead, P.J., and Ankney, C.D. 1984. A critical assumption of band-recovery models may often be violated. *Wildl. Soc. Bull.* **12**: 198–199.
- Weatherhead, P.J., and Ankney, C.D. 1985. Condition and band-recovery data: a reply to Burnham and Nichols. *Wildl. Soc. Bull.* **13**: 349–351.
- Weatherhead, P.J., and Greenwood, H. 1981. Age and condition bias of decoy-trapped birds. *J. Field Ornithol.* **52**: 10–15.
- Whalen, D.M., and Watts, B.D. 1999. The influence of audio-lures on capture patterns of migrant Northern Saw-Whet Owls. *J. Field Ornithol.* **70**: 163–168.

Copyright of Canadian Journal of Zoology is the property of Canadian Science Publishing and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.