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Complete List of Authors:	Lemieux Lefebvre, Sébastien; McGill University, Natural Resource Sciences Landry-Cuerrier, Manuelle; McGill University, Natural Resource Sciences Humphries, Murray; McGill University, Natural Resource Sciences
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Lemieux Lefebvre, S., Landry-Cuerrier, M., Humphries, M. M.

Lemieux Lefebvre, Sébastien¹ : Department of Natural Resource Sciences, McGill University,
21111 Lakeshore, Ste. Anne de Bellevue, H9X 3V9, Canada. Email :
sebastien.lemieux@mail.mcgill.ca

Landry-Cuerrier, Manuelle : Department of Natural Resource Sciences, McGill University,
21111 Lakeshore, Ste. Anne de Bellevue, H9X 3V9, Canada. Email : manuelle.landry-cuerrier@mcgill.ca

Humphries, Murray M. : Department of Natural Resource Sciences, McGill University, 21111
Lakeshore, Ste. Anne de Bellevue, H9X 3V9, Canada. Email : murray.humphries@mcgill.ca

Corresponding author : Lemieux Lefebvre, Sébastien: Environmental and Wildlife Management,
Vanier College, 821 Sainte-Croix, Saint-Laurent, Canada, H4L 3X9. Tel. (514) 903-6530. Email:
lefebvr@vaniercollege.qc.ca

¹ Current Affiliation: Environmental and Wildlife Management, Vanier College, 821 Sainte-Croix, Saint-Laurent, Canada, H4L 3X9. Tel. (514) 903-6530. Email: lefebvr@vaniercollege.qc.ca

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Abstract

Identification of critical habitat is central to major conservation laws protecting endangered species in North America and around the world. Yet the actual ecological research that is required to identify which habitats are critical to the survival or recovery of species is rarely discussed and poorly documented. Here we quantitatively assess the information and methods used to identify critical habitat in the recovery strategies of 53 vertebrates at risk in Canada. Of the CH identifications assessed, 17% were based habitat occupancy information, 28% on habitat characteristics and/or functions and 40% assessed habitat suitability by linking functional use and biophysical characteristics. However, only 15% of the recovery strategies we evaluated examined relationships between habitat and population viability, abundance, individual fitness, or survival. Furthermore, the breadth of evidence used to assess critical habitats was weaker among long-lived taxa and did not improve over time. Hence, although any approach used to identify CH is likely to be a step in the right direction in minimally protecting and maintaining habitats supporting critical life-cycle processes, there is a persistent gap between the widely recognized importance of critical habitat and our ability to quantitatively link habitats to population trends and individual fitness.

Key words: Critical habitat, species at risk, Species at Risk Act, behaviour, habitat use, habitat selection, functional habitat, individual fitness, population survival, recovery target.

Introduction

In recent decades, the identification of critical habitat (CH) (or similar concepts) has been central to major conservation laws protecting species at risk in North America (United States: Endangered Species Act (ESA), Canada: Species at Risk Act (SARA)) and around the world (Australia: Environment Protection and Biodiversity Conservation Act, Europe: European Commission Habitat Directive, UK: Biodiversity Action Plan). The definition of this concept takes different forms, but generally describes the legal obligations of identifying and protecting habitats essential to the conservation of species at risk. In Canada, critical habitat is defined in SARA as “*the habitat that is necessary for the survival or recovery of a listed wildlife species*”, where “listed” refers to species with a Threatened or Endangered status (SARA 2002). This focus on CH follows evidence that habitat loss, fragmentation, and degradation are the main drivers of modern species extinction, range contractions, and population declines (Dirzo and Raven 2003). Identifying and conserving CH is thus considered an essential step in the recovery of species at risk (Taylor et al. 2005). However, despite their recognized importance, the identification of CH requires highly detailed information on habitat characteristics and the life-cycle processes they support and how access or lack of access to a given habitat impacts the population trend and recovery. In general, the process of CH identification is complex and inconsistent, with many species at risk still awaiting the mandatory legal designation of their CH (Hagen and Hodges 2006; Taylor and Pinkus 2013; Favaro et al. 2014).

Designation of CH combines both ecological and legal processes (ESA, SARA, EPBC), and difficulties in reconciling these two aspects are seen by some as the main cause for designation failures (Smallwood et al. 1999; Hagen and Hodges 2006; Hodges and Elder 2008; Greenwald et al. 2012). Differences in threats faced by species at risk, the socio-economic and political context, and conservation priorities of regulatory agencies have all been recognized as

difficulties in the CH designation process (Hagen and Hodges 2006; Knight et al. 2008). Camaclang et al. (2015) reviewed the link between criteria used to identify CH and ecological and legal covariates in the United States, Canada, and Australia, and showed that both aspects influenced the information (e.g. occupancy of habitat or population viability) considered during CH identification. However, legislations involved in the CH identification process vary markedly among the different countries (Camaclang et al. 2015) making it difficult to assess the role of ecological covariates in CH identification independent of the socio-economical-political context of designations. As such, the ecological process of the CH identification– the science needed to identify those habitats that are critical to the persistence and recovery of species at risk – has received much less attention.

Under the Canadian SARA, CH is identified in the recovery strategy, a planning document that identifies the “*goals, objectives and approaches to recover threatened, endangered and extirpated species*”, and mandatorily in the subsequent action plan, which describes “*the measures to take to implement recovery strategy*” (www.sararegistry.gc.ca). As specified in SARA (2002), CH should be identified based on the “*best available information*” which includes all relevant scientific, community and Aboriginal traditional knowledge available at the time of the assessment. In cases where data are insufficient, the government has the obligation to conduct, within five years following publication of the recovery strategy, the research necessary to acquire the information and perform the analyses relevant to CH identification. An advantage of the identification of CH in Canadian recovery strategies is that no socio-economic aspects are considered at this stage of the process, such that CH identification is based solely on the ecological knowledge available for the species considered (DFO 2016). Although various approaches to CH identification have been suggested by the Canadian government (Randall et al. 2003; DFO 2004; Environment Canada 2004; DFO 2007, 2008),

specific guidelines to this effect have only recently been developed and solely for aquatic species (DFO 2016). Based on these guidelines, CH identifications must include the habitat functions and related biophysical characteristics (termed habitat “features” and “attributes”) supporting all essential life-cycle processes of the listed species and an estimate of the required amount of habitat to attain specific population recovery and distribution targets.

Recovery strategies, in which CH are identified, have to be prepared for species that vary widely in their ecological and life-history traits. Canadian vertebrates at risk, for instance, include species such as the Hooded Warbler (*Setophaga citrina* (Boddaert, 1783)), a 10 g, arboreal, insectivorous bird, and the blue whale (*Balaenoptera musculus* L., 1758), a 100 t, marine, planktivorous mammal. The extent, scale and quality of ecological knowledge seems sure to vary according to a species’ natural history, the ecosystem in which they occur, and the methodological limitations and research opportunities they present (Carr et al. 2003; Stergiou et al. 2005; Johnson 2007; Hodges and Elder 2008). Despite these differences, SARA prescribes that the identification of CH of every species be based on high quality data quantifying the relationship between habitat quality, individual fitness and long-term population abundance (DFO 2004; Rosenfeld and Hatfield 2006; Environment Canada 2009; Mooers et al. 2010). However, for the vast majority of species, directly quantifying the link between habitat characteristics and individual survival and population abundance is challenging and, in general, more indirect information is employed as a proxy for habitat quality (Johnson 2007). It is however unclear what type of information is presently used in Canadian CH identifications, and by which ecological and methodological factors they are influenced (Hagen and Hodges 2006; Hodges and Elder 2008).

We here review the information and methods used in studies identifying CH of Endangered and Threatened vertebrate species in Canada, and classify the studies based on the

type of data and analyses used to assess habitat quality and their relatability to individual fitness and population dynamics. We further assess whether the quality of the information used for CH identification varies over time or according to the taxonomy, conservation status, generation time, habitat type, foraging ecology and amount of research realised on the listed species.

Methods

We used the Canadian SARA registry site (www.sararegistry.gc.ca) to determine the status of all vertebrate populations at risk (referred as designatable units, hereafter *DU*, by the Committee on the Status of Endangered Wildlife in Canada and representing the biological units for which conservation status is evaluated), the availability of a finalized recovery strategy (as of March 13, 2017) and its date of publication. All recovery strategies published before April 2017 were examined to determine if CH was identified as part of this step. In cases where CH could not be determined as a result of data deficiency, action plans were examined, when they existed, to determine whether CH was subsequently identified. Description of the information and methods used to identify CH was usually taken directly from the recovery strategy (or action plan), but if other documents were cited in association with CH identification, these were also examined to confirm the methodology.

In peer-reviewed literature, information and methods used to identify CH include deductive modelling based on presence-only data (GREGG and TRITES 2008), logistic models combining presence/absence data with habitat predictors (Turner et al. 2004), functional habitat identification based on behavioural observations (Williams et al. 2009), development of habitat suitability indices from space use and biophysical data (Heath and Montevercchi 2008) and Bayesian modelling of habitat to population abundance relationships (Carroll and Johnson 2008). Thus in general, approaches used for CH identification can be viewed along a continuum of data

quality and associated methodologies (Randall et al. 2003; Rosenfeld and Hatfield 2006; DFO 2008).

We assigned approaches used for CH identification to five categories along this quality of information continuum (Table 1). Category 1 identifications were limited to habitat occupancy data, such as presence only or presence/absence data, residency patterns, kernel densities or frequency data. Category 2 identifications included information on habitat biophysical characteristics and/or habitat functions (such as spawning, breeding, rearing and feeding), but did not link the two. Category 3 identifications linked biophysical and functional characteristics into an analysis of habitat suitability. Category 4 identifications related habitat extent and population viability to determine the amount of CH considered necessary for DU survival and recovery. Category 5 identifications related habitats (size, characteristics, etc.) to population demographics and/or individual fitness measures (reproduction, survival, and abundance) (Table 1).

The CH identifications described in recovery strategies of Canadian vertebrates were scored from 1 to 5 based on the categories described above, to evaluate the general thoroughness and quality of each assessment. Since categories represented a continuum, this semi-continuous variable was reflective of the variety of information and methods used for CH identification, which was assumed to reflect the overall quality of the assessment. These quality scores of CH identification (hereafter *CH scores*) were used to study the relationship (see model details below) between the CH scores and potential ecological correlates of the listed DU, including *taxonomy*, *extent of occurrence*, *area of occupancy*, *body size*, *generation time*, *habitat*, and *diet breadth*, as well as non-ecological correlates, including *date of recovery strategy*, the *DU conservation status*, and two *indices of research effort* (Table 2).

Ecological correlates were extracted from status report documents produced by the Committee on the Status of Endangered Wildlife in Canada (<http://www.cosewic.gc.ca>) during

the listing process, and to a lesser extent recovery strategies. These documents provided the necessary information for all species included in the analysis, except for, in some cases, body size. The main habitat used by species was divided into aquatic (freshwater or marine), ground-dwelling, above ground-dwelling, and semi-aquatic (modified from Davidson et al. 2009; Jones et al. 2009). Some partially fossorial species (e.g. *Taxidea taxus jacksoni* (Schantz, 1946)) were considered ground-dwellers. Atlantic salmon (*Salmo salar* L., 1758) were assigned to aquatic freshwater habitat because the critical habitat of the DU included in our study is only identified for the portion of their life-cycle occurring in that habitat. Semi-aquatic inhabitants included species for which essential parts of their life cycle are dependent on both terrestrial (or arboreal) habitats and freshwater (or marine) habitats. Diet breadth was calculated based on the number of dietary sources exploited (i.e., terrestrial invertebrates, aquatic invertebrates, terrestrial vertebrates, aquatic vertebrates, vegetation, algae and lichen/fungi (adapted from McNab 1986; Owens et al. 1999)). Amphibians were considered as aquatic vertebrate preys.

Non-ecological correlates included year of publication of the recovery strategy, conservation status of the DU (i.e. Threatened or Endangered), and intensity of past scientific research efforts on a species. Year of publication was expressed relative to 2006, i.e., the publication year of the first recovery strategy included in our analysis. Intensity of research efforts was estimated in two ways, first by entering the scientific name of the species into the “topic” search term of the Web of Science database and recording the total number of articles returned, and second by entering the scientific name of the species and the term “habitat” into the “topic” search term of the Web of Science database and recording again the total number of articles returned. The underlying assumption of using this index is that research on behaviour and habitat requirements contribute to understanding ecological factors related to CH of a DU, regardless of the population studied.

The relationship between potential ecological and non-ecological correlates (predictors) and CH identification quality scores (dependent variable) was examined using generalized linear models from the package *nlme* in R (R Development Core Team 2013). For species with multiple DU (including identified CH and sufficient information available on correlates), one DU was randomly selected and included in the generalized linear models. When multiple species are included along with biological and ecological factors in linear models, the potential confounding effect of similarities due to common descent is normally taken into account by using independent contrast (e.g. Cooper et al. 2008) or mixed models (Sodhi et al. 2008). In our case, we wanted to examine taxonomic variation in approaches used to identify CH, and thus included the taxonomic category *class* as a fixed effect, and assessed the potential confounding effect of phylogeny by incorporating an interaction term between taxonomy and other independent variables.

Assumptions of linearity and normality of residuals, and of homogeneity of variance were tested after excluding collinear variables (Zuur et al. 2009). Model selection was based on relative likelihoods of candidate models and the Akaike Information Criterion with a correction for small sample size (AICc) (Burnham and Anderson 2002). As top models AICc weights were below 0.9 (Table 3), we followed an all-subset approach with model averaging to compare model parameters (Burnham and Anderson 2002, 2004; Arnold 2010; Burnham et al. 2011).

Results

Two hundred and forty-two vertebrate populations (i.e. designatable units) were listed under SARA at the time of our analysis, including 158 with a Threatened or Endangered status and a requirement for identification of CH (Fig. 1). A finalized recovery strategy, which under SARA legal requirement should be completed within one or two years after a species is listed as Endangered or Threatened respectively, was available for 100 (63%) of the vertebrates DU, 60

(60%) of which contained an identification of CH (Fig. 1). As only one designatable unit (DU) per species was included in the analysis, seven DU from five species were randomly excluded from the final analysis, resulting in the inclusion of a total of 53 species (S1¹).

Of the 53 CH identifications assessed, 9 (17%) were based on habitat occupancy information, 15 (28%) on habitat characteristics and/or functions, and 21 (40%) on identification of suitable habitats (Fig. 2). Only six (11%) studies established a link between habitat and population viability, whereas only two (4%) included information on the relationship between habitats and population demographics and/or individual fitness.

The mean CH scores attributed to each CH identification was 2.57 ($n = 53$, $SD = 1.03$) and a median of 3. Collinearity led to the exclusion of four variables (*extent of occurrence*, *research effort intensity*, *body mass* and *main habitat*) from the models. Out of 150 models tested, the model including only *Generation Time* was the most parsimonious. According to this model, the log of *Generation Time* ($Z = -2.371$, $p = 0.017$) show a significant negative relationship with the CH scores and thus a decrease in CH identification assessment quality for species with longer generation times (Table 3). Two other competing models presented a delta AICc of 2 or less with this model and included either *Status* or *Date of Recovery Strategy* in addition to *Generation Time* (Table 3). However, model-averaging revealed that only *Generation Time* was significant and had a high weights ($w = 0.84$) indicating a high probability that the top model was the best model (Symonds and Moussalli 2011).

Discussion

Within our 2006-2017 survey period, 100 Canadian vertebrates had a finalized recovery strategy, but only 60 had their critical habitat formally identified. Many of these CH

¹Supplementary material 1, Table S1. : Sources and values of the predictors used in the generalized linear models.

identifications were based on descriptions of habitat occupancy, biophysical characteristics, and/or function, and only a very few (15 %) established habitat-population viability or habitat-fitness associations. Hence, although the identification and protection of critical habitats is a central element of Canada's Species at Risk Act, the critical habitats of most listed vertebrates are either unidentified or identified using limited methods. In general, the methods used for critical habitat identification have not improved over the last several decades (Fig. 3) and are weaker for species with long generation times than for species with short generation times.

Information about habitat occupancy forms the basis of most CH identifications. Almost a fifth (17%) of the CH identifications presented in the reviewed recovery strategies were restricted to descriptions of used habitats and their general characteristics, without any additional ecological information. This assessment approach can be appropriate when distributions and densities reflect habitat quality (Gregs and Trites 2008), but not if animals occur at high abundance in sink habitats or in any other situations where presence or abundance is a misleading indicator of habitat quality (Van Horne 1983; Battin 2004). However, if precautionary approaches prevail and the total extent of the habitats used by a DU are classified as critical habitat, this area of occupancy approach can provide strong protection (DFO 2007, 2016).

Most of the CH identifications went beyond basic descriptions of used habitats and of their general characteristics, to the identification of selected biophysical characteristics using habitat or resource selection analysis and/or by identifying habitat functions from behavioural studies. Habitat selection and behaviour are a product of individual choices, which have presumably been shaped by evolutionary selection and fitness optimization (Pyke 1978; Morris 1992), and are influenced by external factors, including the distribution of food resources (Arthur et al. 1996; Myrsetrud and Ims 1998), intra- and interspecific interactions (Rosenzweig 1981; Morris 1987; Rodriguez 1995; Young 2004), predation risk (Gilliam and Fraser 1987; Creel et al.

2005; Frair et al. 2005) and group size (Fortin et al. 2009). Because habitat selection and behaviour are closely linked to individual fitness and survival, as well as population size (Pyke 1978; Morris 1992; Morris et al. 2009; McLane et al. 2011) they are more likely to successfully identify critical habitats that will support population recovery.

However, adequate protection of the ecological processes that maintain the critical life-cycle requirements of a population requires going beyond habitat selection analysis to identify the specific biophysical characteristics on which each habitat function depends. Almost forty percent of the CH assessments took this additional step by including information on the link between biophysical characteristics (attributes and features) and at least one function that the habitat supports. In our classification, approaches were assigned to this category if at least one function was identified, however critical habitat designations should consider the full suite of functions that support essential life-cycle processes. This information can then further be used to 1) monitor effects of habitat changes on life functions, 2) determine the role of unused habitats in maintaining habitat features and attributes necessary for population recovery and 3) identify habitats that could be restored or recolonized in the context of population recovery (Rosenfeld and Hatfield 2006; Courrat et al. 2009; Richardson et al. 2010). Essential life-cycle processes occurring outside of the geographical mandate of the assessment, such as migration or seasonal residency, would however need to be protected by other jurisdictions, as SARA only applies to Canadian territory.

Identifying the biophysical characteristics that support habitat functions can thus be used to delineate CH more precisely and to recognize activities likely to destroy CH (DFO 2016). In fact, this seems to be the assumption under which CH identifications are currently developed in Canada, i.e. identification and protection of critical habitats is assumed to improve the recovery and survival of the species. Ideally, CH identifications should include quantitative measures of

the amount of habitat necessary to attain population size and distribution objectives (Rosenfeld 2003; Camaclang et al. 2015; DFO 2016). However, only eight (15 %) of the recovery strategies reviewed directly linked habitat to measures of population viability, demographics and/or individual fitness. For example, the CH identification with the highest quality score included a spatially-explicit population demographic model that predicted long-term habitat productivity and population objectives (Heinrichs et al. 2010). Species with long generation times require longer study periods to reliably assess population abundance and viability (Reed et al. 2003). We observed a negative relationship between generation time and the quality of critical habitat assessment, which is suggestive of the difficulties of linking habitats to population viability in long-lived species but also the opportunity to do better among species with short generation times.

SARA has been implemented relatively recently, and the difficulties of quantitatively linking habitat and population viability appears to be a common and persistent limitation in the recovery process (Johnson 2007; Camaclang et al. 2015). If critical habitats are identified using a method that does not link habitat availability and use to population viability, demography, or fitness, there is a key evidence gap that diminishes our assessment of their importance and of the forms of protection required. The manner in which a habitat is identified establishes the framework for its protection (DFO 2016). Establishing the habitat-dependency of individual fitness and population demographics is challenging for many species, especially long-lived ones, and requires considerable research that necessitates time and money. One approach is intensive, short-term research focused on critical habitat, prompted by the listing of a species and the development of a recovery strategy. An alternative approach is continuous and long-term monitoring of habitats and the species that occupy them. While less targeted, this approach is pro-active rather than reactive, and provides the double benefit of early-detection of a population

decline and an immediate and long-term understanding of how habitat change contributed to the decline. A third benefit of the long-term monitoring approach is that species share habitats, meaning that habitat monitoring provides information relevant to the assessment and recovery of many species. A fourth benefit is the opportunity to follow an adaptive management approach, whereby our understanding of the associations between habitats and populations can be improved and expanded through trial and error and adjustment over time.

Despite the increase in the number of CH identifications in recent years, our results show that the quality of the information on which CH identifications are based has not improved over time (Fig. 3), with the earlier recovery strategies including similar information and methods as more recent assessments. To increase this quality, approaches measuring habitat-population viability or habitat-fitness associations, such as those developed for some aquatic species (Vélez-Espino et al. 2010), would need to be developed for other vertebrates species-at-risk. Meanwhile, CH still needs to be promptly identified to ensure the survival and recovery of many species at risk and the highest-priority is to conduct these identifications using the best information and methods possible given currently available scientific knowledge. Our review suggests that information on habitat functions and supporting characteristics can be readily obtained for many species in a manner that will contribute to the SARA requirement of protecting essential life-cycle processes (Environment Canada 2009). However, continuous and long-term monitoring of both habitats and species can offer even more to the identification of critical habitats, and ultimately the recovery of threatened and endangered species in Canada.

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Table 1. Summary of the categories used to classify and score critical habitat (CH) identification assessments presented in recovery strategies.

Category	Classification criteria	CH Score
Habitat occupancy	Critical habitat (CH) identification was based on studies reporting measures of the designatable unit (DU) habitat use, such as presence only or presence/absence data, residency patterns, kernel densities or frequency data.	1
Habitat characteristics and/or functions	CH identification was based on habitat biophysical characteristics (i.e. attributes and features) found within the area of occupancy of a DU and known to be selected preferentially by the species. AND/OR CH identifications was based on habitat functions, i.e. on occurrence of behaviours representing essential life-cycle processes (such as spawning, breeding, rearing and feeding) in the habitats occupied by the DU.	2
Habitat suitability	CH identifications was based on analyses linking the habitat biophysical characteristics (attributes and features) to the essential habitat function(s) they support, in order to identify suitable habitats within the area of occupancy of the DU.	3
Population viability	CH identifications that included analyses of the relationship between the habitat extent and population viability to determine the amount of CH considered necessary for the DU survival and recovery.	4
Population demographics and/or individual fitness	CH identifications that included quantitative analysis relating habitats (size, characteristics, etc.) to population demographics and/or individual fitness measures (reproduction, survival, and abundance) of the DU.	5

Table 2. Variables evaluated as potential correlates of critical habitat identification assessments (CH scores).

Ecological correlates	Description
Extent of occurrence	The area included in a polygon without concave angles that encompasses the geographic distribution of all known populations of a wildlife species.
Area of occupancy	The area within 'extent of occurrence' that is occupied by a taxon, excluding cases of vagrancy.
Body size	Body mass (g) or body length converted to body mass.
Generation time	Average age (year) of parents of a cohort.
Main habitat	Freshwater, marine, ground-dwelling, above ground-dwelling, semi-aquatic.
Diet breadth	Number of food categories composing the main diet.
Non-ecological correlates	Description
Date of recovery strategy	Last publication date of the recovery strategy
Status	Endangered or Threatened
Research effort intensity	Number of Web of Science articles returned based on species scientific name
Habitat research intensity	Number of Web of Science articles returned based on species scientific name and the term “habitat”

Table 3. Structure, AICc weights, AICc values and Δ AICc for competing generalized linear models. Model one was retained as the optimal model (equation shown).

Models	Weights	AICc	Δ AICc
1. Score ~ Generation Time Score = $0.54 + (-0.32) * \log(\text{Generation Time})$	0.16	151.6	0
2. Score ~ Generation Time + Status	0.09	152.7	1.1
3. Score ~ Generation Time + Date of Recovery Strategy	0.06	153.6	2

Table 4. Results from model-averaging for parameter coefficients and relative weights.

The Actinopterygii class was used as the reference category.

	Coefficients	Std. Error	Z value	<i>p</i> value	Weight
Generation Time	-0.34	0.14	2.28	0.02	0.84
Status	0.26	0.26	0.99	0.32	0.34
Date of recovery strategy	-0.02	0.06	0.37	0.71	0.25
Habitat research intensity	-0.03	0.22	0.12	0.91	0.25
Area of Occupancy	0.00	0.10	0.05	0.96	0.25
Diet breadth	0.03	0.15	0.20	0.85	0.24
Class (Amphibia)	-0.65	0.52	1.21	0.22	0.02
Class (Aves)	-0.20	0.35	0.58	0.56	0.02
Class (Mammalia)	-0.25	0.39	0.64	0.52	0.02
Class (Reptilia)	-0.28	0.45	0.62	0.54	0.02

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Figure captions:

Figure 1. The distribution of vertebrate species at risk in Canada, indicating a) at risk status, b) if Endangered or Threatened, whether or not they have a recovery strategy, and c) if they have a recovery strategy, whether or not a critical habitat has been identified.

Figure 2. Frequency distribution of approaches used to identify the critical habitat (CH) of Canadian vertebrates at risk. The approach categories are described in more detail in Table 1 and increase in quality from left (habitat occupancy is low quality and is assigned a CH score of 1) to right (population demographics and individual fitness is high quality and is assigned a CH score of 5).

Figure 3. The quality of approaches used to identify critical habitats (1 is low, 5 is high, see Table 1 and Figure 2 for category descriptions) in vertebrate recovery strategies finalized between 2006 and 2017, where circle size indicates the number of strategies assigned to a given category in a given year and the dashed line indicates the absence of a significant change in quality across the time series (see Table 4 for model-averaged coefficients).

Figure 1.

Figure 3. The quality of approaches used to identify critical habitats (1 is low, 5 is high, see Table 1 and Figure 2 for category descriptions) in vertebrate recovery strategies finalized between 2006 and 2017, where circle size indicates the number of strategies assigned to a given category in a given year and the dashed line indicates the absence of a significant change in quality across the time series (see Table 4 for model-averaged coefficients).

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