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Different responses of congeneric consumers to an exotic food resource: who gets the novel resource prize?

Yvette K. Ortega · Leigh F. Greenwood · Ragan M. Callaway · Dean E. Pearson

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Abstract Exotic species can provide abundant food resources for native consumers, but predicting which native species will respond positively remains a challenge. We studied the foraging behavior of black-capped (*Poecile atricapillus*) and mountain (*P. gambeli*) chickadees in western Montana to compare the degree to which these congeric and syntopic consumers exploited larvae of *Urophora*, an exotic biological control insect living within the seedheads of the invasive forb, spotted knapweed (*Centaurea stoebe*). Chickadees typically forage within tree or shrub cover, whereas knapweed and hence *Urophora* larvae thrive in open grassland away from cover. We found that black-capped chickadees were much more likely than mountain chickadees to forage for *Urophora*. Black-capped chickadees strategically minimized time spent in open habitats by flying out from cover to retrieve knapweed seedheads and immediately returning to cover to extract the larvae. Black-capped chickadees also employed an atypical hovering technique nearly twice as often as their congeners did, particularly when foraging away from cover. Via this hovering technique, birds were able to gather knapweed seedheads from erect plants rather than searching for seedheads on the ground. These shifts in foraging behavior allowed black-capped chickadees to exploit *Urophora* larvae to a much greater degree than their congeners while minimizing exposure to a high-risk habitat, an outcome with potentially important community-wide consequences. Behavioral flexibility has been used to predict the success of invading species. We suggest that behavioral flexibility may also be used to predict how native species will respond to invasions, particularly the availability of exotic food resources.

Keywords Behavioral plasticity · Biological control agent · Food subsidy · Foraging behavior · *Urophora*

Y. K. Ortega (✉) · D. E. Pearson
Rocky Mountain Research Station, USDA Forest Service, 800 E. Beckwith Ave., Missoula, MT 59801, USA
e-mail: yortega@fs.fed.us

L. F. Greenwood · D. E. Pearson
Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

R. M. Callaway
Division of Biological Sciences, Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA

Introduction

Exotic species can have strong negative effects on native species through competition, consumption, and parasitism (Levine et al. 2003; Salo et al. 2007; Pysek et al. 2012), but less appreciated is the fact that such invaders can also have strong positive effects on native species (Rodriguez 2006). Notably, exotic organisms can provide novel food resources for native consumers (Barber et al. 2008; McCusker et al. 2010; Tablado et al. 2010). Moreover, because exotic organisms often become highly abundant, they can provide enormous

subsidies for native consumers and potentially trigger community-wide effects (Roemer et al. 2002; Noonburg and Byers 2005; Pearson and Callaway 2003). To better understand the net effects of biological invasions on native communities, we need to address the full range of native species responses to invaders, from negative to neutral and positive.

Many studies have documented consumption of exotic food resources by native species (Rodriguez 2006), but predicting which native species will successfully exploit such resources remains a challenge (Sih et al. 2010). Few studies have compared the responses of multiple native consumers to exotic food resources, and fewer still have examined the mechanisms that underlie the variation in native species responses (e.g., Waring et al. 1993; Schummer et al. 2008; Tablado et al. 2010). Morphology and physiology determine whether or not a native organism has the capacity to respond to a novel resource. However, given the physical capacity, behavior can provide the flexibility that may be necessary to exploit such novelty (e.g., Greenberg 1990; Lefebvre et al. 1997). Hence, this flexibility may be key to understanding much of the variation in native species responses to exotic food resources (Sih et al. 2010, 2011). Comparative studies of closely related consumers exhibiting differing responses to exotic food resources would provide insight into how behavior influences such variation.

A number of studies have documented the importance of behavioral flexibility and associated behavioral traits in mediating the success of invasive species in new ranges (Holway and Suarez 1999; Sol et al. 2008; Pintor et al. 2009). However, the role that these behavioral attributes have in determining the response of native species to invasions has received relatively little attention. This information gap likely arises from an emphasis on the negative impacts that invaders have on native species (Rodriguez 2006). Yet, if behavioral flexibility allows some invaders to thrive in the novel conditions of a new range, it may also allow some natives to thrive in the novel conditions created by species invasions. Avian species vary greatly in the flexibility of their foraging behavior (Greenberg 1990; Lefebvre et al. 1997), and associated traits such as neophobia (avoidance of novel objects or situations) and innovation propensity (solving novel food problems) correlate with the success of species introduced into new ranges and ecosystems (Sol et al. 2002, 2005a; Martin and Fitzgerald 2005; Møller 2009). Whether exotic or native, behavioral flexibility may confer advantages on organisms faced with novel conditions (Greenberg 1990; Sih et al. 2010, 2011). Hence, understanding such flexibility may help to predict which native species will successfully exploit exotic resources and which will not.

One notable exotic resource in western North America is supplied by the gall flies *Urophora affinis* and *U. quadrifasciata*, which were introduced for the biological control of the Eurasian forb spotted knapweed (*Centaurea stoebe*) in the 1970s (Story et al. 1987). These flies oviposit in knapweed seedheads, and their larvae overwinter in galls and feed on their host plant's tissues (Story et al. 1987). Because *Urophora* successfully established but failed to reduce populations of their very abundant host, they occur at extremely high densities (Story et al. 1995). Furthermore, *Urophora* larvae serve as a winter food subsidy that can double or triple native deer mouse (*Peromyscus maniculatus*) populations (Ortega et al. 2004; Pearson and Fletcher 2008), leading to a variety of complex indirect food-web effects (Pearson and Callaway 2003, 2006, 2008). Native songbirds may be similarly affected. Several songbird species consume *Urophora* larvae during winter (Story et al. 1995; Pearson et al. 2000), and food availability can have strong effects on songbird populations by influencing overwinter survival (Brittingham and Temple 1988; Desrochers et al. 1988; Mccallum et al. 1999) and the onset of breeding (Boutin 1990; Marshall et al. 2002; Ortega et al. 2006). Thus, *Urophora* has great potential to provide a critical resource for some native bird species. However, we have not examined how utilization of this exotic resource varies among taxa, or the role behavioral flexibility might play in this variation.

In western Montana, black-capped chickadees (*Poecile atricapillus*) prey heavily on *Urophora* larvae in the winter (Story et al. 1995). This native songbird typically forages for arthropods, seeds, and fruit within the cover of trees (Hill and Lein 1988; Foote et al. 2010). However, knapweed and hence *Urophora* larvae are much more abundant in open grassland away from the cover of trees (Metlen et al. 2012), forcing the birds to venture into open microhabitats to exploit the exotic food source (Story et al. 1995). Mountain chickadees (*Poecile gambeli*) generally breed at higher elevations than black-capped chickadees, but some overwinter with their congeners in mixed-species flocks within low-elevation woodlands

typically invaded by knapweed. Mountain chickadees have been observed consuming *Urophora* larvae but seemingly take less advantage of this novel resource than black-capped chickadees (L. Greenwood, *pers. obs.*). Mountain chickadees are the closest relative of black-capped chickadees, and these species are very similar in morphology and physiology (Mccallum et al. 1999; Foote et al. 2010). Like black-capped chickadees, mountain chickadees tend to forage for arthropods and seeds within tree cover (Hill and Lein 1988; Mccallum et al. 1999). Therefore, like their congeners, mountain chickadees would have to leave their typical foraging habitat to access concentrations of *Urophora*.

One notable difference between black-capped and mountain chickadees is the breadth of foraging techniques documented for each species. Both species are typically gleaners, taking prey from foliage or bark while perching or hopping, and both have been reported to remove insects from galls in this manner (Abrahamson et al. 1989; Mccallum et al. 1999). However, only black-capped chickadees are known to incorporate a variety of foraging techniques, including hovering and hawking, when pursuing native foods (Robinson and Holmes 1982; Foote et al. 2010). In contrast, mountain chickadees typically show little diversity in foraging behavior (Mccallum et al. 1999). Hence, these two species are quite similar, except that black-capped chickadees express a broader range of foraging behaviors.

We studied the overwinter foraging behavior of black-capped and mountain chickadees in western Montana to compare the extent to which this pair of congeneric, syntopic consumers exploited the novel food resource represented by *Urophora*. We targeted closely-related consumers to control for differences in physiology and morphology and focus on behavioral mechanisms that might influence interspecific variation in exploitation of exotic food resources. Given the documented differences in the foraging flexibility of these consumers, we predicted that black-capped chickadees would exploit *Urophora* to a greater degree than mountain chickadees.

Materials and methods

Study sites were open woodlands near Missoula, Montana. Two sites in the Bitterroot River drainage (elevation 945 m, 46°50′08.19″N 114°5′58.20W, 46°49′52.02N 114°5′52.68W) were dominated by ponderosa pine (*Pinus ponderosa*), while the third site in Marshall Canyon 10 km northwest of Missoula was a dry upland habitat (elevation 1,220 m, 46°54′21.56″N 113°55′28.12W) consisting primarily of ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*). Forest cover was intermixed with the native shrubs red-osier dogwood (*Cornus stolonifera*) and ninebark (*Physocarpus malvaceus*). Open areas contained native grassland species including bluebunch wheatgrass (*Psuedoroegnaria spicata*), Idaho fescue (*Festuca idahoensis*), and a variety of native forbs (Lackschewitz 1991). The primary exotic plant, spotted knapweed, was scattered throughout the study sites and particularly abundant in open grassland patches. All three sites were located at least 1 km from human habitation to minimize effects of backyard feeders on foraging behavior.

Field work was conducted January through May 2006, and December 2006 through April 2007. This period encompassed most of the chickadee non-breeding season and most of the period when *Urophora* larvae are available within knapweed seedheads (Story et al. 1995). Each study site included the home range of at least one mixed-species flock of overwintering passerines, typified at low elevations in western Montana by black-capped chickadees, mountain chickadees, red-breasted nuthatches (*Sitta canadensis*), pygmy nuthatches (*Sitta pygmaea*), and occasional woodpeckers (Family Picidae). Flocks were lured into mist-nets using playback of chickadee mobbing calls and a taxidermy-mounted great-horned owl (*Bubo virginianus*) or northern saw-whet owl (*Aegolius acadicus*). We marked each bird with a unique combination of a USFWS aluminum band and three color bands. A total of 30 black-capped chickadees and 13 mountain chickadees were resighted during foraging observations. Each individual was primarily associated with a single site. Although 30 % of the banded birds at the two Bitterroot River sites (separated by 0.5 km) were observed at both sites, only 15 % of foraging observations were associated with a secondary site. The total number of banded birds using each site as its primary site was: Bitterroot 1, $n = 9$ black-capped and $n = 7$ mountain; Bitterroot 2, $n = 16$ black-capped and $n = 4$ mountain; Marshall Canyon, $n = 5$ black-capped and $n = 2$ mountain.

One or two observers visited each site at least once per week, rotating sequentially through the sites. During each visit, observers first located a mixed flock by ear. Individuals from the flock were then selected randomly for observation, except that non-banded birds were only sampled when a banded bird could not be located. Each observation session was restricted to 2-min per bird after which a new individual was selected, and birds could be resampled during a visit. During observation sessions, we used a digital voice recorder to continuously log foraging behaviors and food processing behaviors. Food types were identified via direct observation or association with characteristic foraging or processing behaviors according to the following categories: seeds (primarily conifer), *Urophora* larvae (within knapweed seedheads), native arthropods, and other. *Urophora* larvae are the only arthropod found to overwinter within knapweed seedheads in western Montana (based on dissection of seedheads; Pearson et al. 2000; Ortega et al. 2012). Arthropods other than *Urophora* were associated with native trees and assumed to be of native origin given that the tree species in our study area are not known to be infested with exotic arthropods (A. Gannon, State Entomologist, Montana DNRC, *pers. comm.*). We classified foraging techniques as gleaning (obtaining stationary food while perched, hopping, or hanging upside down) or hovering (obtaining stationary food while flying). Processing behaviors entailed handling of food items, primarily removal of seedcoats from conifer seeds and extraction of *Urophora* larvae from knapweed seedheads. For each foraging or processing location, we also recorded the substrate (trees and shrubs to species, ground, or knapweed plant), height of the bird, distance to the nearest tree or shrub (not recorded for *Urophora* foraging events prior to March 2006), and cover of spotted knapweed within a 5-m radius, categorized as follows: none, <5, 5–25, 26–50, and >50 %. Bird observations were primarily limited to the zone below 12 m, as it was difficult to discern color-band combinations and maintain visual contact with birds above this height.

Statistical analyses

We used generalized linear mixed models (PROC GLIMMIX, SAS version 9.3) for most analyses comparing foraging behavior between species or food types (i.e., native or *Urophora*). Means from these analyses are reported as least squares means with associated SEs. In these models, we treated the individual bird as the independent sampling unit by including random factors to account for covariance among observations (1) per individual and (2) per individual and visit. Observations from non-banded individuals were therefore excluded. Site was included as a random factor. We treated year as a fixed factor, as well as the interaction of year with the fixed factor of interest (i.e., species or food type). However, these interaction terms were excluded from final models given lack of significance ($P > 0.05$). We used a binomial distribution to test for interspecific differences in the probability of each of the following events: foraging for native arthropods versus seeds (observations of the "other" category were limited to carrion and excluded from analyses due to the small sample size of $n = 2$), foraging for native food in trees or shrubs versus on the ground, foraging for *Urophora* versus native foods, and obtaining *Urophora* via hovering versus ground foraging. Where sample size permitted, we also used a binary distribution to test for within-species differences in the probability of foraging in or out of cover by food type (i.e., native food or *Urophora*). To compare foraging height for native food types between species, we used a mixed model with a normal distribution. Although foraging height was positively skewed, log transformation did not alter results so we report statistics for the untransformed variable.

Mixed models for interspecific comparison of foraging and processing of native foods in versus out of cover did not converge, presumably because models were too complex for the data (most observations fell into one category), so we instead used a χ^2 test for homogeneity of variance or Fisher's exact test when expected counts were <5 in any cell (PROC FREQ, SAS version 9.3). This was also the case for (1) interspecific comparisons dealing with processing of *Urophora* and (2) use of *Urophora* foraging techniques in versus out of cover. Additionally, we used a χ^2 test or Fisher's exact test to test whether the distribution of foraging observations among knapweed cover categories differed (1) between *Urophora* and native food types for each species, respectively, and (2) between chickadee species for *Urophora* and native food types, respectively. Observations from non-banded birds were included in χ^2 related analyses because repeated sampling of individuals could not be

accounted for. Hence, the scale of inference is limited to the foraging observation for these analyses.

Results

The general composition of the native portion of the diet did not differ significantly between chickadee species ($F_{1,41} = 0.5$, $P = 0.48$), as measured by the probability of birds foraging for arthropods versus seeds (black-capped: $\bar{x} = 88 \pm 2.2$ %; mountain: $\bar{x} = 90 \pm 2.8$ %). Both species foraged for native food items exclusively by gleaning (black-capped: n = 870 observations, mountain: n = 311 observations), primarily from the foliage or bark of trees and less often shrubs, but also from the ground. The probability of individuals foraging for native resources in trees or shrubs versus on the ground did not differ between species (black-capped: $\bar{x} = 86 \pm 3.1$ %, mountain: $\bar{x} = 87 \pm 4.3$ %; $F_{1,40} = 0.1$, $P = 0.83$). Foraging height associated with native foods averaged 4.1 ± 0.33 m for black-capped chickadees and 4.7 ± 0.5 m for mountain chickadees, and did not differ between species ($F_{1,41} = 1.1$, $P = 0.3$). Chickadees foraged for native resources within tree or shrub cover in 98 % of cases, with no difference between species ($\chi^2_1 = 1.0$, $P = 0.31$, n = 1,034). Additionally, birds processed native foods while perched in trees or shrubs in 99 % of cases, with no difference between species (Fisher's exact test, $P = 0.3$, n = 165).

Despite these similarities between consumers, the foraging behavior of the two chickadees diverged greatly with respect to the exotic food resource. Most importantly, the probability of foraging for *Urophora* larvae as opposed to native foods was much greater ($F_{1,40} = 37.0$, $P < 0.001$) for black-capped ($\bar{x} = 28 \pm 12.9$ %) compared to mountain chickadees ($\bar{x} = 2 \pm 1.6$ %). When foraging for *Urophora*, the chickadees used a technique not employed for native foods in our study: they hovered above knapweed plants to remove seedheads either with their feet or with their bill. Otherwise, they gleaned seedheads that had fallen on the ground [except in 2 cases of n = 378 where a black-capped chickadee either plucked seedheads from an old American robin (*Turdus migratorius*) nest composed of knapweed or perched on a knapweed plant to remove larvae from seedheads]. Notably, black-capped chickadees favored hovering over ground gleaning ($\bar{x} = 92 \pm 4.8$ %), whereas mountain chickadees were much less likely to use the hovering technique ($\bar{x} = 31 \pm 27.1$ %; $F_{1,23} = 6.0$, $P = 0.022$).

Although black-capped chickadees rarely foraged for native foods away from tree or shrub cover, they often ventured away from such cover to access *Urophora* larvae (Fig. 1). Indeed, for this chickadee species, the probability of foraging away from cover averaged 54 % (±8.3 %) when the food source was *Urophora* larvae compared to only 2 % (±0.8 %) for native foods ($F_{1,44} = 69.4$, $P < 0.001$). Black-capped chickadees tended to stay within 1 m of cover when foraging for *Urophora*, but they ventured farther in 24 % of cases (n = 187), to a maximum distance of 20 m (Fig. 1). Black-capped chickadees used hovering more often when obtaining seedheads in open microhabitats versus beneath the cover of trees or shrubs ($\chi^2_1 = 4.3$, $P = 0.038$, n = 182; Fig. 2). For mountain chickadees, we could not examine this due to low sample size, but 3 of n = 6 relevant observations occurred away (1–2 m) from cover.

Both chickadee species favored tree or shrub cover when processing the exotic resource, as seen with native resources. After obtaining a single knapweed seedhead via hovering or ground gleaning, individuals flew to a perch within cover to remove *Urophora* larvae rather than removing them where collected in 92 % of cases, with no difference between species

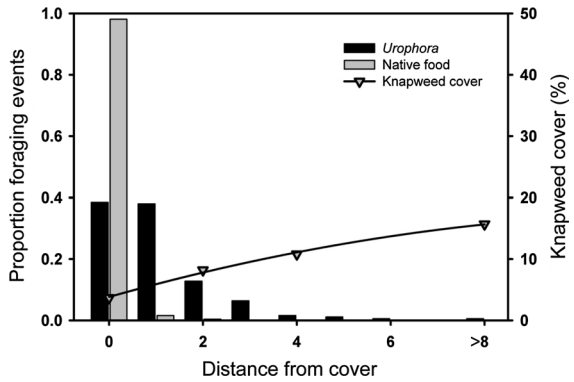

Fig. 1 Distance (1-m intervals) black-capped chickadees foraged from tree or shrub cover to obtain *Urophora* larvae as opposed to native food resources in western Montana, 2006–2007. Also shown is mean cover of spotted knapweed (*Centaurea stoebe*) measured under tree cover and at varying distances from cover in similar woodland habitats in western Montana (after Metlen 2010)

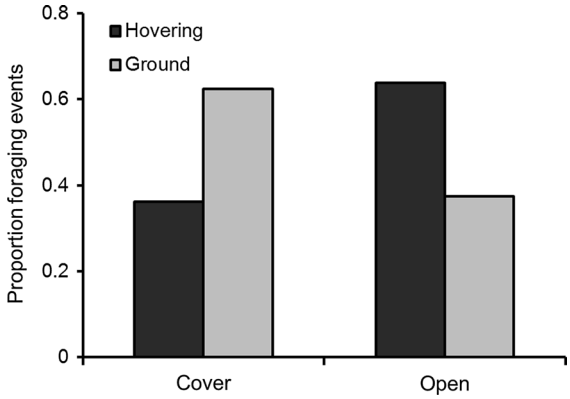

Fig. 2 Black-capped chickadee use of hovering and ground gleaning techniques when foraging for *Urophora* larvae in tree or shrub cover versus in the open (away from cover) in western Montana, 2006–2007. Data for each foraging technique are presented in terms of the proportion of foraging events occurring in each microhabitat

($\chi^2_1 < 0.1$, $P = 0.9$, n = 498). Similarly, 96 % of *Urophora* processing cases occurred within cover, with no difference between species ($\chi^2_1 < 0.1$, $P = 0.82$, n = 482).

For both species, foraging for native foods occurred primarily in locations with <5 % knapweed cover in the understory, whereas foraging for *Urophora* larvae occurred primarily in locations where knapweed cover exceeded 50 % (black-capped: $\chi^2_4 = 405.1$, $P < 0.001$, n = 1,220; mountain: Fisher's exact test, $P < 0.001$, n = 319; Fig. 3). Use of knapweed cover categories when foraging for native foods differed significantly between species ($\chi^2_4 = 20.7$, $P < 0.001$, n = 1,128), as driven by low cover categories (Fig. 3), but use of knapweed cover categories when foraging for *Urophora* did not differ between species (Fisher's exact test, $P = 0.61$, n = 411).

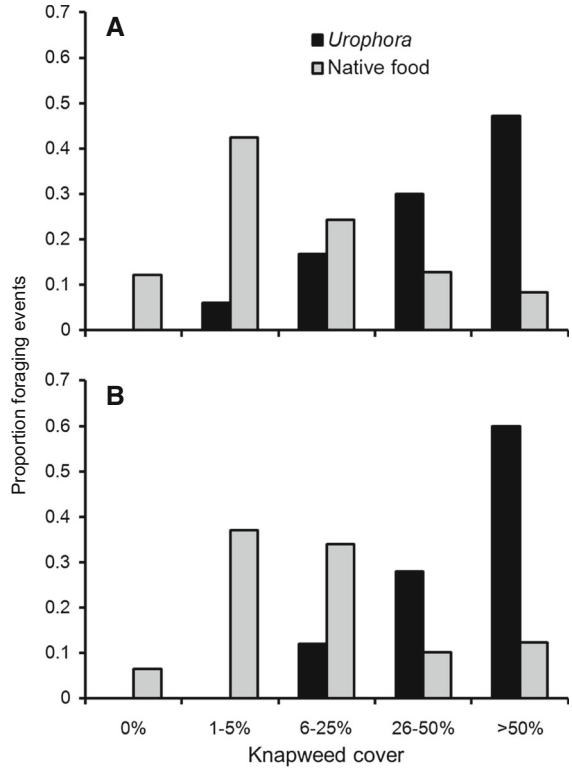

Fig. 3 Black-capped chickadee (**a**) and mountain chickadee (**b**) use of spotted knapweed, by cover category, when foraging for *Urophora* larvae compared to native food resources in western Montana, 2006–2007

Discussion

Exotic species can provide abundant food resources for native consumers capable of exploiting them, but we currently lack the means of predicting which native species should do so and why. We found that two closely related and syntopic consumers diverged greatly in their behavioral response to an introduced food resource. Black-capped chickadees frequently shifted from their typical foraging microhabitat and foraging technique to exploit *Urophora* larvae, whereas mountain chickadees rarely did so. Our results suggest that differing degrees of behavioral flexibility may underlie the divergent response of these consumers to the exotic resource. Although phenotypic differences between species are not in themselves surprising given the nature of speciation and subsequent differentiation (Garland and Adolph 1994), such trait differences may be useful in elucidating how native species may respond to biological invasions.

As introduced organisms, *Urophora* are evolutionarily novel food resources for North American chickadees. However, the basic presentation of this resource, insect larvae living within galls formed by the host plant, is not particularly novel, since both chickadees are known to extract native insect larvae from plant galls (Abrahamson et al. 1989; Mccallum et al. 1999). What is atypical is the microhabitat where the exotic food source is concentrated. Both chickadee species in our study foraged for native foods almost exclusively within tree or shrub cover and primarily

above-ground at an average height >4 m. Similar foraging patterns have been described for these species elsewhere (e.g., Mccallum et al. 1999; Foote et al. 2010). However, spotted knapweed, the obligate host plant for *Urophora* larvae, averages <1 m tall (Pearson et al. 2012) and is most abundant in open grassland vegetation away from overstory cover (Fig. 1, Metlen et al. 2012). Therefore, to truly exploit the exotic food resource, chickadees must expand beyond their typical foraging microhabitat by not only descending to the understory but also moving away from cover.

We found that black-capped chickadees readily made this shift, spending nearly 30 % of their foraging effort on *Urophora* larvae as opposed to native foods, while mountain chickadees foraged for *Urophora* in only 2 % of cases. Black-capped chickadees frequently ventured away from cover to access dense patches of the exotic resource. Strategically, these chickadees usually flew out from cover to obtain a seedhead and then immediately returned to cover to extract the larvae. This behavior underscores the fact that cover was favored over open grassland, likely in response to differing predation risk (Lima 1985). In addition to venturing into atypical microhabitats, black-capped chickadees also employed an atypical foraging technique to exploit *Urophora* larvae. While both species obtained native foods exclusively via gleaning, black-capped chickadees usually hovered above knapweed plants to gather seedheads, particularly when foraging away from cover (Fig. 2). In hovering, black-capped chickadees adopted a technique used only infrequently by this species to pluck native arthropods from foliage (Robinson and Holmes 1982). Black-capped chickadees also gleaned fallen knapweed seedheads from the ground, but the probability of individuals employing this technique versus hovering was <10 %. Hence, by hovering, black-capped chickadees avoided landing on the ground to search for seedheads, presumably also minimizing time spent away from cover and exposure to predators, a response shown in other contexts (Lima 1985). Hovering may also facilitate selection of the most profitable seedheads, as black-capped chickadees can distinguish seedheads containing relatively high densities of larvae (Templeton 2011). In contrast, on the rare occasions when mountain chickadees foraged for *Urophora* larvae, they were roughly a third as likely as their congener to employ hovering, instead favoring the ground-based technique used for native foods. Thus, only black-capped chickadees markedly shifted their foraging behavior to solve an evolutionarily novel problem, and through this innovation, exploited an abundant exotic resource to a much greater degree than their congener.

The divergent response of the congeners to the exotic resource may reflect interspecific differences in behavioral flexibility. Both black-capped and mountain chickadees demonstrated the ability to employ the same atypical behaviors to forage for *Urophora*, underscoring the similarities in morphology and physiology between these sister species. Yet only black-capped chickadees frequently adopted these behaviors to exploit the abundant resource. Neophobia and boldness (exploratory and/or risk-taking behavior) are two key behavioral traits that mediate feeding innovation, governing the ability for some species to opportunistically incorporate novel food types into their diets (Greenberg 1990; Greenberg and Mettke-Hofmann 2001; Webster and Lefebvre 2001; Sol et al. 2011). *Urophora* and knapweed are no longer novel in the sense that chickadees have been exposed to this resource for many generations, but lower neophobia and/or greater boldness in black-capped chickadees could at least in part explain why this species has incorporated the exotic resource into their diet while mountain chickadees largely avoid it (Greenberg and Mettke-Hofmann 2001). The differing migratory status of the congeners could also influence their foraging flexibility (Greenberg and Mettke-Hofmann 2001). Although the congeners overwinter together in mixed-species flocks in our study area, black-capped chickadees are year-round residents whereas mountain chickadees move to higher elevations to breed. Previous work has shown that resident bird species exhibit greater behavioral flexibility than migratory species, with lower neophobia and higher rates of feeding innovation (Sol et al. 2005b; Mettke-Hofmann et al. 2013). Neophobia, boldness, and innovation propensity are also among the behavioral traits distinguishing species that have successfully invaded new ranges or ecosystems from those that have not (Rehage and Sih 2004; Pintor et al. 2008; Sol et al. 2002, 2005a, 2011). However, to our knowledge, this notion of divergent behavioral types or traits has seldom been used to examine the varied response of native taxa to exotic species (Sih et al. 2004, 2010, 2011).

The proximate or ultimate degree of predation risk is thought to be an important determinant of foraging opportunism (Greenberg 1989; Greenberg and Mettke-Hofmann 2001; Sol et al. 2011). Accordingly, mountain chickadees may have been more likely than black-capped chickadees to avoid open microhabitats with high densities of *Urophora* larvae if they were more vulnerable to predation than their congener in these microhabitats. Chickadees respond to predation threats by taking refuge in trees or shrubs, and birds removed from cover are exposed to greater predation risk (Lima 1985). The key to birds evading predators in flight is maneuverability, which is constrained by wing span and body size (Dial 2003; Templeton et al. 2005). Therefore, black-capped chickadees could be less vulnerable to predation than their congener due to their shorter wing span and smaller body size, although differences in these parameters appear small (average wing chord differs by <5 %, average tarsus length by <10 %; Mccallum et al. 1999; Desrochers 1985). Alternatively, the congeners could differ in vulnerability to predation due to their use of different *Urophora* foraging strategies. The hovering technique favored by black-capped chickadees should minimize predation risk by facilitating rapid return to cover. Mountain chickadees may tend more towards the ground-gleaning technique and hence be constrained in their foraging behavior because they are less adept at hovering (e.g., due to small differences in morphology; Moreno et al. 2001), and/or are more rigid in their use of the standard foraging technique, as also suggested by previous studies documenting relatively stereotyped foraging behavior in this species (e.g., Foote et al. 2010). Finally, mountain chickadees may fail to exploit *Urophora* because they are more risk-averse than their congeners, potentially reflecting exposure of these species to differing levels of predation pressure outside of the overwinter period and/or over evolutionary time scales (Greenberg and Mettke-Hofmann 2001).

A second factor that could underlie the divergent responses of black-capped and mountain chickadees to the exotic resource is dominance hierarchies. Mountain chickadees are known to be subordinate to black-capped chickadees in mixed winter flocks across age and sex classes (Grava et al. 2012). Previous work on sparrows hypothesized that socially subordinate species may avoid foraging in open microhabitats because they are more vulnerable to attack by dominant species when away from cover (Greenberg 1989; but see Schneider 1984). Similarly, dominance by black-capped chickadees could limit mountain chickadee access to the exotic resource. Dominance status within and between chickadee species has been shown to influence access to food resources (Desrochers 1989; Grava et al. 2012). If black-capped chickadees prevented mountain chickadees from accessing *Urophora*, then agonistic interactions should have been more common in *Urophora*-rich microhabitats (e.g. Desrochers 1989; Grava et al. 2012). To address this, we checked our database for agonistic interactions (chases or displacement), which were recorded during foraging observations. Of the limited agonistic interactions we observed, all occurred within trees or shrubs, primarily while birds were foraging for native resources ($n = 26$ of 34 observations), and all were intraspecific (black-capped: $n = 32$; mountain: $n = 2$). We never saw black-capped chickadees physically preclude mountain chickadees from accessing *Urophora*, although it is still possible that the risk imposed by the dominance of the former species caused avoidance of the resource by the latter. Regardless, the dominance relationship may further reflect the divergent behavioral types apparently represented by the two species. For many animal taxa including chickadees, dominance status of individuals has been positively associated with aggressiveness as well as boldness (Fox et al. 2009). Moreover, aggressiveness and boldness are among the correlated traits that appear to promote the success of select species where novel conditions are concerned (Holway and Suarez 1999; Rehage and Sih 2004; Pintor et al. 2008).

Exploitation of *Urophora* larvae could translate to population-level benefits for black-capped chickadees. Survival of temperate zone songbirds, including chickadees, is typically food-limited in winter (Brittingham and Temple 1988; Desrochers et al. 1988; Mccallum et al. 1999). Food availability also influences the onset of breeding and hence reproductive performance in many bird taxa (Boutin 1990; Marshall et al. 2002; Ortega et al. 2006). Moreover, both overwinter survival and reproduction promote population size (Samson and Lewis 1979; Boutin 1990; Holmes et al. 1996). Thus, it would not be surprising if black-capped chickadee populations increased because of the abundant exotic resource (e.g., Ortega et al. 2004; Pearson and Fletcher 2008), potentially leading to a variety of community-level impacts

including negative effects on native competitors or prey (e.g., Roemer et al. 2002; Pearson and Callaway 2003, 2006, 2008). Alternatively, positive effects of *Urophora* on black-capped chickadees may be negated if individuals suffer increased predation rates when foraging for the exotic resource, which is more abundant in open and hence high-risk microhabitats. However, black-capped chickadees appeared to mitigate the risk imposed by these microhabitats by adopting a foraging strategy that minimized time spent away from cover.

Behavioral flexibility may be a hallmark of species particularly capable of adjusting favorably to novel conditions. If so, behavioral flexibility may provide a predictive framework that elucidates not just which species will become invasive, but also how native species will respond to exotics (Sih et al. 2010, 2011). Such understanding could also be used to assess which biocontrol introductions are likely to trigger indirect nontarget food subsidy effects (Pearson and Callaway 2003, 2005). Applying this framework to understand the responses of two congeneric, syntopic species to an abundant insect introduced for weed biocontrol, we correctly predicted that the consumer exhibiting a wider range of foraging behaviors in past studies would exploit the novel resource to a greater degree. Our work suggests that appropriate trait-based frameworks historically applied to predict invasiveness may also be used to predict the response of native species to invasions.

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