BLACK-CAPPED CHICKADEES SELECT SPOTTED KNAPWEED SEEDHEADS WITH HIGH DENSITIES OF GALL FLY LARVAE

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Abstract. Chickadees and tits excel at identifying and exploiting novel food sources. One such food source in western North America is the larvae of *Urophora* gall flies (Diptera: Tephritidae), which were recently introduced to help control the spread of spotted knapweed (*Centaurea maculosa*). In winter, Black-capped Chickadees (*Poecile atricapillus*) of many western populations spend much of their time foraging exclusively on this new and rich food source. Because the number of gall flies within knapweed seedheads varies, I examined whether chickadees preferentially selected seedheads with high densities of prey. In large, semi-natural, outdoor aviaries, I presented bouquets of knapweed seedhead to chickadees and allowed them to forage until approximately half of the seedheads were removed. Seedheads rejected by chickadees had significantly fewer larvae than did seedheads not exposed to chickadee predation, indicating that chickadees had selected and removed seedheads with high densities of gall flies. Seedhead size was positively correlated with the number of insects housed within, and chickadees preferentially removed larger than average seedheads while foraging. These results indicate that size is one reliable cue that chickadees might use to select seedheads with high gall fly density. However, chickadees were more successful at selecting seedheads with higher larval density than expected if they used size alone, which suggests that these birds may also use other cues to further increase their foraging efficiency. This study demonstrates the types of subtle decisions chickadees and other birds make even when foraging on relatively novel food sources.

Key words: biological control, chickadee, foraging, gall fly, invasive species, knapweed, non-target effects, prey selection.

Poecile atricapillus Selecciona Capítulos de *Centaurea maculosa* con Alta Densidad de Larvas de la Mosca *Urophora*

Resumen. Algunas especies de la familia Paridae tienen una extraordinaria capacidad para identificar y explotar recursos alimenticios nuevos. Uno de estos recursos alimenticios es la larva de la mosca *Urophora* (Diptera: Tephritidae), que induce la formación de agallas en plantas. Esta mosca fue introducida recientemente para ayudar a controlar la expansión de la planta invasora *Centaurea maculosa* en el oeste de América del Norte. Durante el invierno, los individuos de *Poecile atricapillus* de varias poblaciones del oeste pasan gran parte del tiempo forrajeando sobre este nuevo y rico recurso alimenticio. Debido a que el número de larvas de moscas varía entre los capítulos de cada planta, examiné si los individuos de *P. atricapillus* seleccionaron preferentemente capítulos con alta densidad de presas. En aviarios externos seminaturales, expuse a individuos de *P. atricapillus* a buqués de capítulos de *C. maculosa* y permití que las aves forrajearan hasta que aproximadamente la mitad de los capítulos fueran consumidos. Los capítulos rechazados por las aves tuvieron significativamente menos larvas que los capítulos no expuestos a la depredación de las aves, indicando que los individuos de *P. atricapillus* seleccionaron y removieron los capítulos con altas densidades de agallas con larvas de *Urophora*. El tamaño del capítulo se correlacionó positivamente con el número de insectos contenidos en él, y los individuos de *P. atricapillus* removieron preferentemente capítulos más grandes que el tamaño promedio cuando forrajeaban. Estos resultados indican que el tamaño de los capítulos es una señal confiable que las aves utilizan para seleccionar los capítulos con alta densidad de moscas. Sin embargo, las aves presentaron un mayor éxito de selección de capítulos con mayor densidad de larvas que lo esperado si sólo usaran el tamaño del capítulo como método de identificación, lo que sugiere que estas aves podrían usar también otras señales para aumentar su eficiencia de forrajeo. Este estudio demuestra el tipo de decisiones sutiles que los individuos de *P. atricapillus* y de otras especies pueden hacer, incluso cuando están forrajeando sobre recursos relativamente nuevos.

INTRODUCTION

Chickadees and tits (family Paridae) are generalist and opportunistic foragers. Although they feed primarily on insects during the breeding season, outside the breeding season these birds expand their diet to include up to 50% food other than insects (Smith 1991). Winter foods are diverse and include insects, spiders, snails and slugs, seeds, berries, roosting bats, tree sap, dead fish, and animal fat from carrion (Smith 1991, del Hoyo et al. 2007). These birds also use anthropogenic food sources,

frequently visiting seed, suet, or peanut feeders, opening milk bottles, or even taking food directly from people (Smith 1991, del Hoyo et al. 2007). The success of parids may be partly due to this dietary flexibility and ability to discover and exploit hidden or novel food sources (del Hoyo et al. 2007).

One novel food source that has recently become available to the Black-capped Chickadee (*Poecile atricapillus*) is gall flies of the genus *Urophora* (Diptera: Tephritidae). *Urophora affinis* and *U. quadrifasciata* are two of the 13 species of insects that have been introduced in North America to help control the spread of spotted knapweed (*Centaurea maculosa*) (Harris 1980, Lang et al. 2000). This knapweed is a perennial forb (family Asteraceae) that was introduced from Eurasia in the early 1900s and has since spread to nearly every state and has become one of the most widely established invasive species in the Pacific Northwest of North America (Maddox 1979, Sheley et al. 1998). It uses a variety of impressive physical and chemical methods, such as compensatory growth and phytotoxic allelochemicals, to outcompete native plants (Marler et al. 1999, Ridenour and Callaway 2001, Bais et al. 2002). It has invaded grasslands, prairies, and savannas, as well as disturbed areas, such as roadsides and pastures (Sheley et al. 1998), where it forms dense monospecific stands (Ridenour and Callaway 2001). Gall flies help control knapweed by laying their eggs within tight clusters of knapweed flowers, called seedheads or capitula, during the summer. As each larva grows, it induces formation of a gall, in which it overwinters. Gall formation reduces seed production; larvae in a seedhead can reduce a knapweed's seed output by 75–95% (Story et al. 2008).

The introduction of gall flies has helped slow the spread of knapweed, but it has also affected birds and mammals. Gall flies can reach very high densities (Myers and Harris 1980), creating an extraordinary new food source for native predators, and the effects of this rich food source can be seen across multiple trophic levels. For example, introduction of gall flies has changed the population dynamics and densities of deer mice (*Peromyscus* spp.; Pearson et al. 2000, Ortega et al. 2004), which in turn affect the prevalence of hantavirus (Pearson and Callaway 2006).

Chickadees frequently feed on gall flies in the winter, and high densities of gall flies in stands of knapweed provide them an important food source. Because chickadees are small birds with high energy requirements and typically live in northern latitudes with harsh climates, a rich food source, such as these gall fly larvae, may increase their winter survival (Smith 1991, Olson and Grubb 2007). Chickadees forage on gall fly larvae by breaking off a single knapweed seedhead in flight and carrying it back to a tree, where they then handle the seedhead with their feet, using their bill to extract the larvae (Story et al. 1995). Chickadees typically remove a single seedhead from the plant during each foraging trip and usually select this seedhead quickly from above without landing on the plant.

Because of the high density of gall flies, chickadees may spend more than half of their foraging time extracting gall flies each day (Story et al. 1995). However, the rate of infestation of knapweed seedheads is highly variable: a single seedhead can contain anywhere from 0 to 24 larvae (Story et al. 1995).

Because chickadees select a single seedhead with each foraging trip, and travel time is presumably nontrivial (Schoener 1979), they could improve their efficiency by selecting seedheads that have high densities of gall flies. In a field study, Story et al. (1995) observed that chickadees remove seedheads with higher than average densities of gall flies. It is unclear, however, how chickadees make these decisions. In this study, I experimentally examined whether chickadees select seedheads with high densities of gall flies and tested one mechanism that chickadees might use to make their foraging decisions.

METHODS

Using mist nets and playback of the "chick-a-dee" mobbing alarm call (Smith 1991, Templeton et al 2005, Templeton and Greene 2007), I captured wintering flocks of Black-capped Chickadees near Missoula, Montana (46° 50′ N, 114° 02′ W). I captured five different flocks each composed of six individual chickadees of mixed age and sex. Each flock was consecutively housed in a $16 \times 16 \times 4$-m outdoor aviary at the University of Montana's field research station at Fort Missoula for 1 to 2 months in the winter from 2001 to 2003. The aviary contained numerous live trees and snags to provide a natural habitat. Chickadees were fed mealworms, sunflower seeds, hard-boiled eggs, and peanuts, all of which were hidden in the vegetation and woody cavities throughout the aviary to help simulate a natural context for foraging. In addition, I periodically provided "bouquets" of flowering stalks of knapweed, with each stalk containing up to 60 flowering heads, from which chickadees extracted insect larvae. Although knapweed flowers and leaves die back in winter, dried stalks with the old flowering heads (seedheads) remain through much of the winter. Most seeds disperse in late summer, but the seedheads contain overwintering gall fly larvae in the winter.

First, I tested whether chickadees select seedheads with high densities of insects by allowing chickadee flocks to forage on bouquets of knapweed seedheads. I collected flowering stalks containing about 200 total seedheads from plants (usually around five or six different plants) surrounding the research station, where gall flies are well-established. I split these seedhead bouquets into two groups, presenting about 2/3 to chickadees and reserving 1/3 as a control from which I estimated the natural density of gall flies in the population. I placed bouquets of approximately 100 seedheads each in a central location in the aviary, and the chickadees quickly began foraging on this familiar resource. Each bouquet was left in the aviary for approximately 1 hr, until chickadees had removed about 50% of the seedheads (mean = 53 ± 19 SE seedheads remaining per bouquet). To be sure that foraging preferences of certain individuals did not overly affect the data, I used five

different flocks of chickadees (two flocks once each, three flocks twice each, for a total of eight trials; I collected one control sample for each flock, $n = 5$).

I dissected seedheads from both groups by hand under a dissecting microscope and counted the number of *Urophora* maggots in each seedhead. I did not discriminate between *U. affinis* and *U. quadrifasciata*. In total, I dissected 510 seedheads from the bouquets presented to chickadees and 308 seedheads from the control group that was untouched by chickadees. I excluded seedheads that were not fully developed, that were inhabited by other species of insects (uncommon), or that had visible damage. Because chickadees rarely feed on gall flies without removing the seedhead (Story et al. 1995; pers. obs.), visible damage was likely due to another type of predator foraging on the bouquets before I harvested them).

I compared the number of insects in the seedheads after the chickadees' foraging with those in control samples to estimate the effects of chickadee predation on insect abundance. Because counting insects in a seedhead necessitated destroying the seedhead, it was impossible to know insect densities in the initial sample of seedheads before they were presented to chickadees. However, the control sample should be equivalent to a "pre-chickadee" sample because both were collected from the same place at the same time. I used bouquets of seedheads as the sampling unit ($n = 13$; eight post-chickadee and five control) and calculated the average number of larvae per seedhead for each bouquet. Using JMP 7.0 (SAS Institute, Inc), I compared these averages with an independent-samples t-test. Values reported under Results are means $\pm$ SE.

Next, I conducted a second experiment to test one possible mechanism that chickadees might use to select high-density seedheads, namely, seedhead size. I compared the average size of seedheads that I placed in the aviary (pre-) with the average size of those remaining after they were exposed to chickadees (post-), with the difference between these two values representing the size of the seedheads selected and removed by chickadees. To estimate the seedheads' size, I used calipers to measure the largest diameter of each seedhead. Seedheads are umbel shaped, approximately twice as long as in diameter. I first measured each seedhead placing it in the aviary ($n = 6$ bouquets, with 197 ± 25 seedheads each; 1180 seedheads total). I then retrieved seedheads that had not been removed by chickadees and measured the diameter of each remaining seedhead (mean = 81 ± 25 seedheads remaining per bouquet; 486 seedheads total). Again, I averaged the seedheads' size for each pre- and post-treatment bouquet and used the average for a bouquet as the sampling unit in a paired t-test ($n = 6$ pairs) to compare seedhead size before and after chickadee foraging.

Last, I examined whether seedhead size was a reliable indicator of gall fly density. I collected a random sample of seedheads from the same location as the bouquets previously described. I measured the diameter of each seedhead before dissecting it and counting the number of gall flies housed within. I ran a linear regression model to determine the general relationship between seedhead size and number of *Urophora* larvae living in the seedhead ($n = 818$ seedheads). Again, I excluded from these analyses any seedheads that were not completely opened, had other species of biocontrol insects, or appeared damaged.

RESULTS

Seedheads in the control group had on average more than three times the number of larvae per seedhead than those rejected by chickadees ($t_{11} = -3.85$; $P = 0.003$), indicating that foraging chickadees had selectively removed seedheads with insect densities higher than average. Control seedheads averaged 3.32 ± 0.47 larvae per seedhead ($n = 5$ bouquets with 308 total seedheads); those rejected by chickadees averaged 0.99 ± 0.38 larvae per seedhead ($n = 8$ bouquets with 510 total seedheads). Larger seedheads also supported more *Urophora* larvae (Fig. 1; ANOVA: $F_{1,817} = 172.40$, $P < 0.001$). Linear regression explained about 30% of variation in larval density ($y = 1.18x - 4.67$; $R^2 = 0.30$); higher-order models did not improve the fit. After chickadee foraging, the seedheads' average diameter decreased from 5.36 ± 0.26 mm (pre-chickadee; 1180 total seedheads) to 4.38 ± 0.36 mm (post-chickadee; 580 total seedheads) (paired t-test,
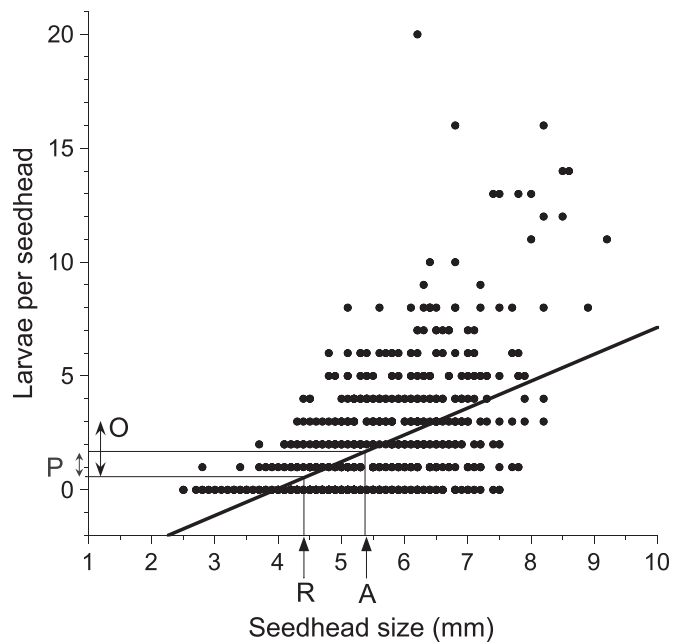

FIGURE 1. Relationship between the size of knapweed seedheads, as measured by the largest diameter of the seedhead, and number of gall fly larvae found within. The regression ($y = 1.18x - 4.67$; $R^2 = .30$, $P < 0.001$) is based on data from a sample of 818 seedheads. The change in the seedheads' average size (see text) from those available ("A"; 5.36 mm) to chickadees to those remaining ("R"; 4.37 mm) after exposure to chickadees, along with the prediction ("P") for a corresponding change in larval numbers after chickadee foraging (1.1 larvae), is depicted with thin lines. The observed ("O") difference in larvae (2.2 larvae) resulting from chickadee foraging is also shown for comparison.

$n = 6$ pairs; $t_5 = -5.87$, $P = 0.002$), indicating that chickadees had selectively removed larger than average seedheads.

I used the relationship between seedhead size and gall fly density to predict how the chickadees' observed behavior (selecting large seedheads) should affect the number of insects a bird could extract from a given seedhead. I used the best-fit regression model (above) to predict chickadee foraging success (y), given their observed selection of seedhead size (x). Chickadees appeared to be more successful in their foraging than predicted by the simple size-based model described above. The average size of seedheads rejected by chickadees was <1 mm smaller than the average size of available seedheads (above). The regression model predicts that this change in seedhead size should correspond with chickadees obtaining 1.1 additional insect per foraging trip (Fig. 1, "P"), as compared with completely random foraging. However, chickadees obtained, on average, 2.2 more insects per seedhead (Fig. 1, "O") than they would if they were foraging randomly. Thus chickadees obtained approximately twice the number of larvae predicted by the simple size rule.

DISCUSSION

Chickadees selected knapweed seedheads with higher than average insect densities, seedhead size reliably predicted the number of insects inside, and while foraging chickadees selected seedheads larger than average. These results corroborate previous field observations of wild chickadees foraging on knapweed gall flies (Story et al. 1995), and suggest that chickadees may use a simple rule based on seedhead size to assess the potential reward for each foraging trip. Because maximizing the rate of energy intake is an important determinant of foraging behavior (Pyke et al. 1977, Krebs et al. 1978), animals often develop simple rules, such as one based on the size of prey, to increase the efficiency of their foraging (Hutchinson and Gigerenzer 2005). For example, Northwestern Crows (*Corvus caurinus*) select only prey that meet minimum size and weight requirements (Zach 1979, O'Brien et al. 2005). Similarly, chickadees also select especially heavy seeds (Heinrich et al. 1997), and when foraging on larvae in goldenrod galls, they focus preferentially on larger galls (Abrahamson et al. 1989).

Like that of goldenrod galls, the size of knapweed seedheads is significantly correlated with insect density; however, size alone explains only about 50% of the variation in gall fly numbers in a seedhead. Chickadees obtain considerably more insects than they would by using seedhead size alone to make foraging decisions, suggesting they may use other cues in addition to seedhead size to fine-tune their foraging efforts. There are several cues that chickadees might use to assess the density of a gall fly infestation. Chickadees have exceptional hearing and pay attention to very subtle acoustic variations in their communication system (e.g., Mennill et al. 2002, Templeton et al. 2005, Lucas and Freeberg 2007), and it is possible that they assess gall fly density by listening to sounds produced by insect movements. Passerine birds' olfaction may be

more highly developed than previously suspected (Zelano and Edwards 2002), and it is possible that chickadees might smell insects inside seedheads. Last, chickadees may be using other visual cues to assess gall fly density, such as counting the number of visible galls, assessing possible variation in the plant's growth form, or selecting seedheads in the topmost branches, where flowers mature earlier and *Urophora* flies frequently lay their eggs (Story and Anderson 1978). Although chickadees might be using any combination of these cues to assess gall fly density, they do not appear to spend much time assessing seedheads: chickadees only rarely stop to examine the potential food source. Instead, they typically removed seedheads in flight, after a direct flight to the knapweed plant from a perch, and with little to no hovering above the plant. That chickadees are able to make such successful foraging decisions with so little time spent assessing seedheads is quite remarkable, and the mechanisms deserve further study.

Equally impressive is the fact that chickadees have learned to exploit this novel food source in such a short time. Although gall flies have been established in North America only since the 1970s chickadees and tits excel at exploiting novel food sources (Sherry and Galef 1984) and can quickly learn to assess food quality by the associated visual cues (Heinrich and Collins 1983). Chickadees can face tremendous energetic challenges in the winter (Smith 1991, Olson and Grubb 2007), and their success in spite of these challenges is likely due in part to their ability to exploit novel food sources efficiently (del Hoyo et al. 2007). In this case, the novel food source is an exotic insect, located on an introduced plant, and has been available in the environment for only 30 years (Story et al. 2008). In this short time, chickadees have learned not only how to take advantage of this unusually rich food source but also how to improve their foraging efforts by selecting only seedheads with greater than average insect densities.

ACKNOWLEDGMENTS

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