

INVASIVE PREY IMPACTS THE ABUNDANCE AND DISTRIBUTION OF NATIVE PREDATORS

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Abstract. While an extensive literature exists on the negative effects of invasive species, little is known about their facilitative effects on native species, particularly the role of invasives as trophic subsidies to native predators. The invasive gypsy moth (*Lymantria dispar*) undergoes periodic outbreaks during which it represents a super-abundant food source for predators capable of consuming it, particularly native cuckoos (*Coccyzus erythrophthalmus* and *C. americanus*). We examined how gypsy moth outbreaks affect the abundance and distribution of cuckoos using the North American Breeding Bird Survey and 29 years of U.S. Forest Service gypsy moth defoliation records. Abundances of both Black-billed and Yellow-billed Cuckoos were significantly above average during outbreaks, but populations were average or below average in preceding and subsequent years, suggesting that cuckoos are immigrating to defoliations during outbreak years. Spatial analyses showed that cuckoo abundances ~40–150 km outside of defoliation areas were significantly below average, and these under-occupied breeding areas extended in all four compass directions around outbreaks. This result supports the idea that cuckoos locate gypsy moth outbreaks during a post-migratory nomadic phase. By shifting the annual distribution of cuckoos, gypsy moths may be shifting the trophic impact of cuckoos across large distances, which could affect native insect herbivores and plants.

Key words: *Coccyzus*; cuckoo; gypsy moth; invasive species; *Lymantria dispar*; outbreak; predation; spatial distribution.

INTRODUCTION

The negative impacts of invasive species are well documented (Vitousek et al. 1996, Mack et al. 2000). They frequently reduce population sizes of native species through competitive interactions (Vilá et al. 2004) or direct predation (Salo et al. 2007). Less attention has been paid to facilitative effects of invasives on native members of their new community. A recent review by Rodriguez (2006) found that facilitation by invasives occurs in a variety of habitats and through a number of mechanisms including habitat alteration, pollination, competitive and predator release, and trophic subsidies, although few examples exist for any one of these areas.

The role of invasives as trophic subsidies is of particular interest because there has been little investigation into the impacts of invasive species on native predators. Because invasives often attain high abundances, they may represent an important food source to native predators capable of exploiting them. Although the phenomenon of natives consuming introduced species is widespread and includes herbivores feeding on nonnative plants (Memmott et al. 2000, Trowbridge

2004), frugivores consuming fruit of alien plants (Witmer 1996, Gosper et al. 2006), and consumers eating nonnative animals (Spencer et al. 1991, Harding 2003, deRivera et al. 2005), rarely have ecologists documented an increase in abundance of the native consumer. Examples include mice feeding on an insect introduced for biocontrol (Ortega et al. 2004) and the well-known case of Golden Eagles (*Aquila chrysaetos* L.) depredating feral pigs (*Sus scrofa* L.) on the California Channel Islands (Roemer et al. 2002).

Two lines of evidence suggest that outbreaks of nonindigenous gypsy moths (*Lymantria dispar* L.) may represent a trophic subsidy for North American cuckoos. First, few birds eat gypsy moth caterpillars, presumably due to their hair-like setae (Forbush and Fernald 1896, Whelan et al. 1989), but cuckoos are often considered “hairy” caterpillar specialists (Hughes 1999, 2001) and may even prefer gypsy moths to native caterpillar prey (Cooper et al. 1990). Historical anecdotes suggest that cuckoo abundances have increased locally during gypsy moth outbreaks (Brewer et al. 1991). One previous study examined cuckoo abundance in relation to gypsy moth outbreaks: Gale et al. (2001) used Breeding Bird Census data from six sites that had experienced defoliations. They found that cuckoo abundances at these sites actually tended to increase one or two years before the year of highest gypsy moth caterpillar abundance, considered to be the outbreak. Second, cuckoos are well known to specialize in

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exploiting insect outbreaks. They have been reported feeding on outbreaks of tent caterpillars (*Malacosoma* spp.) and fall webworms (*Hyphantria cunea* Drury) (Hughes 1999, 2001) and occur at high population densities during periodical cicada emergences (Koenig and Liebhold 2005).

Here we test the hypothesis that gypsy moth outbreaks affect the abundance and distribution of native cuckoos using data from the North American Breeding Bird Survey (BBS) and digitized gypsy moth defoliation records. Specifically, we ask: (1) do cuckoos exhibit a positive numerical response to outbreaks, and (2) does this response vary through space in relation to the outbreak? Our results demonstrate a local increase in abundance of these bird species and suggest that it is due to migration to outbreak sites rather than to an impact on reproductive success.

METHODS

Study species

The gypsy moth (Lepidoptera: Lymantriidae) is a widespread Eurasian species that was introduced to Massachusetts in the 1860s (Forbush and Fernald 1896) and has spread across the northeastern United States and southeastern Canada (Johnson et al. 2006). Outbreaks of gypsy moth are cyclic and occur on an ~10-year cycle, causing large-scale defoliation of deciduous forests (Johnson et al. 2005). Damage by larvae peaked in the early 1980s, with annual defoliation >50 000 km², but more recently defoliations have been less extensive (USDA Forest Service 2008). While the definition of “invasive” is debatable (Richardson et al. 2000, Lockwood et al. 2007), we refer here to the gypsy moth as invasive because it is a nonnative species whose range is expanding and has a significant impact on the structure and processes of its invaded ecosystems.

Two native cuckoo species occur in the northeastern United States, Black-billed (*Coccyzus erythrophthalmus* Wilson) and Yellow-billed Cuckoos (*C. americanus* L.). Both are Neotropical migrants that generally breed from May–September in woodlands, often within areas of dense scrub or thickets (Hughes 1999, 2001).

Data collection and analyses

The BBS is a standardized census of North American birds conducted since 1966. The survey consists of individual transects (“routes”) 39 km in length spread across the United States and Canada. Volunteers record the identity and number of birds seen and heard during 3-min stops at 50 evenly spaced points along the routes (Sauer et al. 2005).

We used digitized maps of gypsy moth defoliation records from 1975 to 2003 provided by personnel at the USDA Forest Service Forestry Sciences Laboratory at Morgantown, West Virginia, USA. These maps were compiled from state defoliation monitoring data by Andrew M. Liebhold; paper maps sketched during annual aerial surveys from each state were scanned

and georeferenced to create a database of northeast U.S. gypsy moth defoliation records. For details of the database and its creation, see Liebhold et al. (1997).

We matched GIS maps of BBS routes with defoliation maps for the years 1975–2003. For each route, any year that a part of the route intersected a defoliation polygon was designated a defoliation year for that route. Each year per route was assigned a year since defoliation (ysd) value. Thus all defoliation years for a route were given a value of ysd = 0, the year immediately following was given ysd = 1 if not defoliated, the next year ysd = 2 if not defoliated, and so on. Given the results of Gale et al. (2001), it was important to include years preceding defoliation as well. For all defoliations that were preceded by at least five non-defoliation years, we assigned ysd = -1 through ysd = -5 for those years.

We downloaded abundance data for both cuckoo species for all routes in states where gypsy moth had established by 2003. We excluded routes on which cuckoos had never been recorded and routes with <10 years of data during the study period. We standardized abundances following Koenig and Liebhold (2005). Because both species have experienced long-term population declines since the BBS was established (Sauer et al. 2005), we removed long-term trends from each route with linear regression. Prior to regression, raw abundances were log-transformed to normalize regression residuals. Residuals from each regression were transformed into *z* scores with mean = 0 and SD = 1. In this way, a standardized abundance of zero can be considered the long-term average abundance of that species for that route. Standardized abundance > 0 indicates an above-average abundance for that route, and standardized abundance < 0 is below average.

To answer our first question, if cuckoos exhibit a positive numerical response to gypsy moth outbreaks, we averaged abundances with the same ysd value within each route, and only routes that included all ysd values from -5 to 10 were retained for analyses (*n* = 81 routes for Black-billed, *n* = 76 for Yellow-billed). Standardized abundances for routes were analyzed with repeated-measures ANOVA with ysd as within-subject factors. Abundance was the response variable and year was the independent variable. The sphericity assumption (an assessment of the circularity of the variance-covariance matrix; von Ende 2001) was violated for Black-billed, so we adjusted the degrees of freedom using the Huynh-Feldt epsilon ($\epsilon > 0.9$).

To determine if the response of cuckoos varied spatially, we included all routes with cuckoos and at least 10 years of data in the invaded states (*n* = 638 for Black-billed, *n* = 630 for Yellow-billed). For each year and route, we obtained the distance from the starting point of each route to the nearest defoliation and the bearing in degrees from the defoliation to the route. Routes were divided into those north (315°–45°), east (45°–135°), south (135°–225°), and west (225°–315°) of the outbreak. For all routes combined, and for each

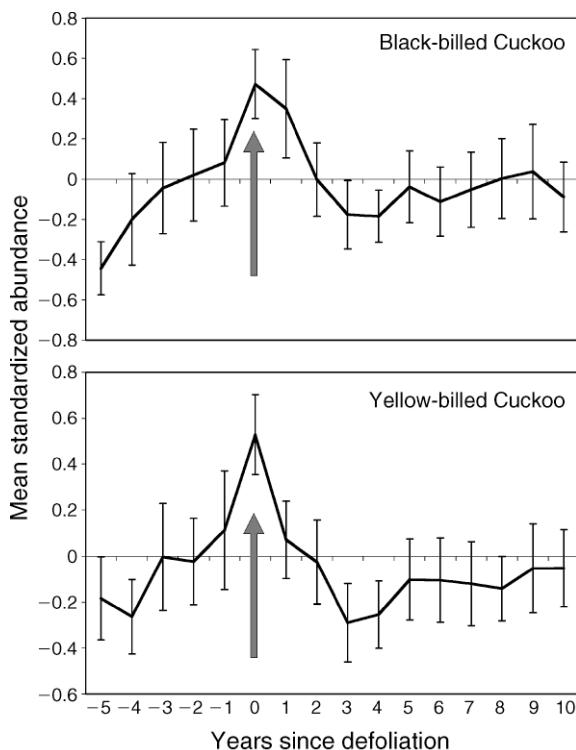


FIG. 1. Mean standardized abundance of cuckoos during and following gypsy moth outbreaks. Error bars show 95% CI, and arrows indicate defoliation years. Here, standardized abundance of 0 is the detrended, long-term average abundance on a BBS (Breeding Bird Survey) route (see *Methods*).

cardinal direction individually, we plotted annual standardized abundance against distance to the nearest defoliation in that year. We fit a LOWESS curve and bootstrapped by resampling the curve 500 times. From these replicate resamples we obtained 95% confidence intervals.

RESULTS

Abundances of cuckoos varied significantly among years since defoliation (Black-billed, $F_{13,3,1066.8} = 7.08$, $P < 0.001$; Yellow-billed, $F_{15,1125} = 9.631$, $P < 0.001$). Both cuckoo species showed a strong, positive numerical response during gypsy moth outbreaks. Abundances in years preceding outbreaks did not differ from average or were below average. The peak in abundance during outbreaks disappeared by the following year in Yellow-billed and by two years in Black-billed (Fig. 1). Abundances of both species were also significantly below average 3–4 years after an outbreak.

The response of cuckoos to defoliations varied spatially in relation to the gypsy moth outbreak. For both cuckoos, abundance at the defoliation site was high but rapidly declined away from the defoliation and was significantly below average from 44 to 159 km away for Black-billed and 40 to 140 km away for Yellow-billed (Fig. 2, top panels).

This spatial response (high abundance at a defoliation but below average at greater distances) was consistent in all directions for both species (Fig. 2, lower panels). The extent of these low abundances varied, but extended as far as 172 km. These patterns were significant (upper bound of 95% CI falls below 0) for all but Black-billed Cuckoos east of defoliations. For distances between 58 and 70 km, Black-billed Cuckoos east of defoliations were marginally less abundant than average (90% CI falls below 0).

DISCUSSION

Gypsy moth outbreaks had a strong effect on the abundance of both Black-billed and Yellow-billed Cuckoos. The number of cuckoos recorded on BBS routes during outbreaks was significantly greater than average route abundance. For Yellow-billed Cuckoos, the number recorded both before and after the outbreak did not differ from, or were below, average, while for Black-billed Cuckoos the second year following the outbreak was also higher. That cuckoos are more abundant in the outbreak year suggests that the numerical response is not the result of an earlier positive local reproductive response. That is, if cuckoos had higher reproductive rates due to the abundant food resource that gypsy moth caterpillars represent, the higher abundances would not be apparent until the year after an outbreak. BBS routes are surveyed in the early breeding season to record adults, and recently fledged juveniles are excluded from counts. Cuckoos may indeed exhibit a positive reproductive response to gypsy moth outbreaks, but such a result is not apparent in our data, except perhaps for Black-billed Cuckoos. Both species declined in abundance in the year after a defoliation, but Black-billed abundances remained significantly above average for that year (Fig. 1). Local banding studies, spanning a pre- and post-outbreak period, would be needed to determine the relative contribution of immigration vs. reproduction to changes in abundance.

These results differ from those of Gale et al. (2001), who found that cuckoos of both species increased at some sites one or two years prior to the major defoliation year of a gypsy moth outbreak. However two of the six sites they examined showed a pattern similar to the current study, in which abundances increased only in the outbreak year. The differences in our results may be due to different methods of designating "outbreak years." Gale et al. (2001) state that gypsy moths were typically present for multiple years at their sites, so they used firsthand accounts by observers to identify the year in which defoliation was most extreme as the outbreak. We designated outbreak years as those in which defoliation was recorded in the defoliation database; defoliation levels of ~30% or greater are necessary for detection (Liebhold et al. 1997). Defoliation levels during outbreak years in Gale et al. (2001) are estimated at 50–100%. Thus in a multiple-year outbreak, Gale et al. (2001) may have considered the

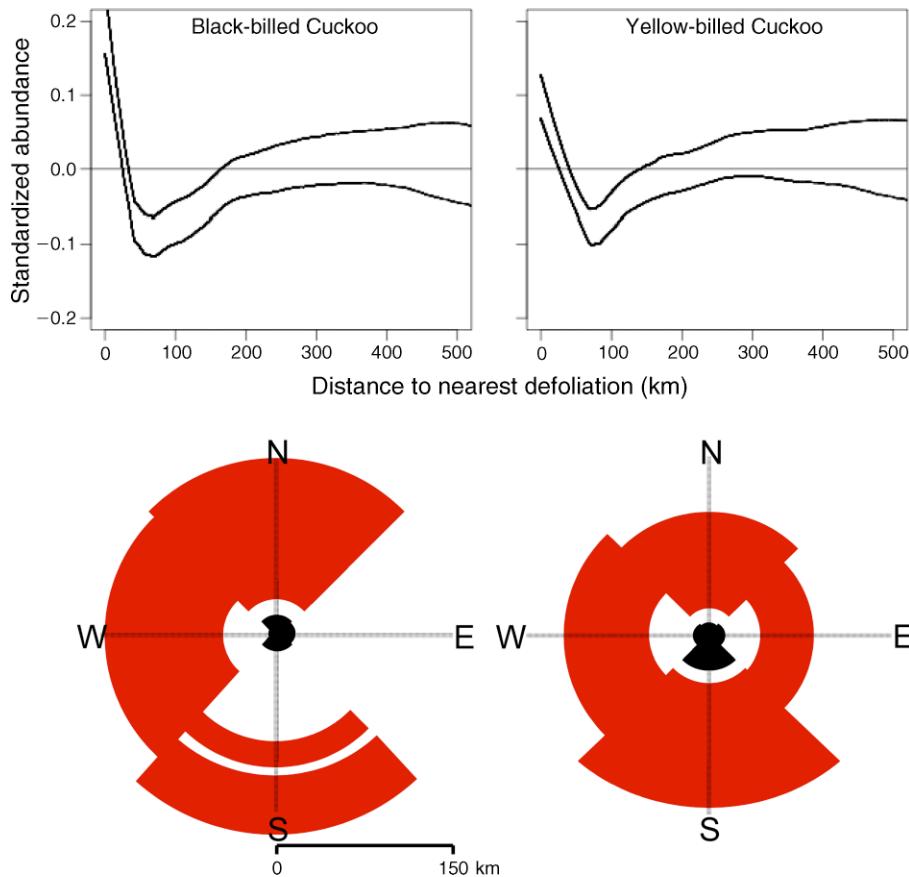


FIG. 2. Distribution of cuckoos in response to gypsy moth defoliation. Top panels are standardized abundance plotted against distance to nearest defoliation. Lines are upper and lower bounds of 95% CI based on bootstrapped replicates of locally weighted regression. Bottom panels are directional distribution relative to nearest defoliation event. The center of the figure represents the location of a hypothetical defoliation. Black regions of the figure are significantly greater than average abundance; red regions are significantly below average abundance; white regions do not significantly differ from average abundance.

earlier years of the outbreak as “pre-outbreak” and only the later, most severely defoliated year as the outbreak itself. Our method would consider all these years as “outbreak years,” while “pre-outbreak years” would be those with no recorded defoliation.

Our spatial analysis suggests that the source of the increased local cuckoo population during an outbreak is the region surrounding defoliations extending tens to hundreds of kilometers away. As these birds move from the surrounding landscape into defoliation areas, they leave presumably suitable nesting sites unoccupied or underoccupied, creating a trough of low abundances outside gypsy moth outbreaks. But if outbreaks “draw in” cuckoos from great distances, how do these birds locate concentrated food resources? Hughes (1999, 2001) proposed that cuckoos enter a “post-migratory nomadic phase” upon reaching their breeding grounds in late spring or early summer, during which they wander across the landscape in search of suitable breeding conditions.

Our data support the existence of this nomadic phase. If cuckoos were simply migrating north in spring and

stopping to nest when they encountered a gypsy moth outbreak, the underoccupied sites would be concentrated to the north of defoliated areas because most birds would stop migrating before reaching these areas. But the trough of low abundances surrounds gypsy moth defoliations, and is actually broader to the south than the north for Yellow-billed Cuckoos and extends farther to the south than to the north for Black-billed Cuckoos. This pattern would be expected if cuckoos wandered across large areas in search of abundant food. Additionally, cuckoos have a delayed nesting phenology relative to most other Neotropical migrants (Hughes 1999, 2001), consistent with the idea of a wandering period in late spring and early summer.

To our knowledge, the only other example of a population shift by a native predator in response to invasive prey is Golden Eagles on the Channel Islands of California. Introduced feral pigs acted as a trophic subsidy, allowing eagles to colonize the islands to the detriment of the eagles’ other choice prey, the endangered island fox (*Urocyon littoralis* Baird; Roemer et al. 2002). The eagles were not present on the islands prior to

1994. This change in eagle distribution led to a restructuring of the islands' food webs and nearly drove the fox to extinction on several islands. In contrast, gypsy moth outbreaks cause a redistribution of cuckoos within their current range, and presumably a redistribution of their predation impact, reducing it in some areas and increasing it in others. The exact strength of the trophic impact of cuckoos on forest food webs is unknown. Insectivorous birds can have important effects, both directly on insect prey (Holmes et al. 1979) and indirectly on plants by consuming herbivorous insects (Marquis and Whelan 1994, Van Bael et al. 2008). Additionally, because cuckoos may specialize on hairy or spiny caterpillars, a gypsy moth outbreak may reduce the predation pressure on native hairy caterpillars in the regions adjacent to the outbreak. At the same time, the outbreak may increase predation on these natives within the outbreak, resulting in apparent competition between the invasive and native insect herbivores. Increased densities of cuckoos could also benefit their own predators and increase transmittance of pathogens and parasites.

This study draws attention to the complexity of interactions between exotic and native species. Nonnatives have caused innumerable declines in native species, but by the very fact that they are embedded within ecological networks, they will have both negative and positive interactions with indigenous species. Positive interactions are recognized as important forces in community dynamics (Bertness and Callaway 1994). These interactions can be either direct consumptive (trophic subsidies) or non-consumptive (e.g., mutualisms) interactions or indirect interactions (e.g., habitat amelioration). Further studies are needed to generalize about the role and effects of nonnative species as trophic subsidies for native predators, particularly when populations of the alien exhibit large fluctuations in the new environment. For example, invasive populations of species as varied as zebra mussels (*Dreissena polymorpha* Pallas; Strayer and Malcolm 2006), house mice (*Mus domesticus* L.; Singleton et al. 2007), and garlic mustard (*Alliaria petiolata* (M. Bieb.) Cavara & Grande; Nuzzo 1999) can vary annually in abundance. During high points in these cycles, they may represent important prey for native consumers and thus affect predator population sizes and community structure in invaded regions.

We do not wish to downplay the threat to biodiversity posed by invasives, yet from the point of view of an organism on the receiving end of these positive interactions, an invasive species could be considered "beneficial." This would seem to be the case for cuckoos and gypsy moths, although verifying this would require observations of nesting success and fledgling survival and comparison to non-invaded areas. Habitat changes due to gypsy moth defoliation, such as a more open canopy due to overstory tree mortality and increased shrub-layer growth, may also benefit understory-nesting bird species like Eastern Towhees (*Pipilo erythrophthal-*

mus L.; Bell and Whitmore 1997, 2000). Nonetheless gypsy moth outbreaks are destructive and can cause severe economic loss through tree mortality and may increase encroachment of red maple (*Acer rubrum* L.) into oak-dominated woodlands (Fajvan and Wood 1996, Jedlicka and Vandermeer 2004). For some birds, gypsy moths may also increase nest parasitism by Brown-headed Cowbirds (*Molothrus ater* Boddaert; Bell and Whitmore 2000).

A more difficult issue is how to view these positive interactions in conservation decision-making and practice. In situations where the nonnative provides a beneficial service to a native species of conservation concern, management decisions should weigh these benefits against potential ecological costs. Thus invasion biology theory needs to incorporate positive interactions and particularly the potential role of invasives as trophic subsidies when considering both the effects and management of invasive species.

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