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Research article

Impacts of Argentine ants on avian nesting success

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Abstract. Biological invasions can have severe and widespread impacts on ecological communities. A few species of ants have become particularly damaging invaders but quantitative data of their impacts on many taxa is still lacking. We provide experimental evidence using artificial nests baited with quail eggs that the invasive Argentine ant (*Linepithema humile*) can be a significant avian nest predator – Argentine ants recruited to more nests and in higher abundance than the native ant species they displace. However, at a site invaded by Argentine ants, we monitored over 400 nests of a ground-nesting species, the Dark-eyed Junco (*Junco hyemalis*), and found that less than 2 % of nests failed as a result of Argentine ant predation/infestation. A review of the literature also suggests that Argentine ants may not be a serious threat to bird nests relative to other predators or parasites. However, invasive ants with the capability of overwhelming prey though stinging (specifically the red-imported fire ant, *Solenopsis invicta*), may have a higher impact on avian nesting success.

Keywords: Ant invasions, Argentine ants, *Linepithema humile,* red imported fire ant, *Solenopsis invicta*

Introduction

Biological invasions are often associated with negative impacts on natural communities (Parker et al., 1999). Despite the ever-increasing awareness of the effects of invasive species, identifying the ecological consequences of invaders is still essential to prioritize limited time and resources. Moreover, it is not always clear if the impacts associated with the establishment and spread of an invasive species are directly attributable to the invasion or rather the result of confounding factors such as habitat modification which may facilitate the invasion process (Suarez et al., 1998).

Ants have become inadvertently introduced to nearly every island and continent in the world (McGlynn, 1999; Suarez et al., 2001). In the United States, at least two species have become widespread, economically costly, and ecologically damaging: the red imported fire ant (*Solenopsis invicta*) and the Argentine ant (*Linepithema humile*). In addition to displacing native ants and disrupting arthropod communities, these species may negatively effect vertebrate populations through two processes. First, by displacing and disrupting arthropod communities, invasive ants can have bottom-up effects by changing the availability and distribution of food resources (Suarez et al., 2000; Suarez and Case, 2001; Allen et al., 2001). Second, through direct predation and antagonism, invasive ants may act as predators, creating a top-down effect (reviewed in Wojcik et al., 2001, Holway et al., 2002).

Reduced nesting success is one of the primary mechanisms thought to underlie the decline of songbirds in the United States (Robinson et al., 1995). While many studies suggest that invasive ants, specifically the Argentine ant and the red imported fire ant, may act as important nest predators, most accounts are anecdotal and limited to few observations (reviewed in Holway et al., 2002). Moreover, it is often unclear if nesting success is significantly reduced in invaded areas relative to un-invaded areas. In this paper, we examine the effects of Argentine ants on avian nesting success in southern California. First, we use an artificial nest experiment to determine if Argentine ants are a greater threat to bird nests than the communities of native ants they displace. Second, we examine the impacts of Argentine ants on the nesting success of a ground nesting bird, the Dark-eyed Junco (*Junco hyemalis*). We compliment this data by reviewing the literature on the impacts of invasive ants on avian reproductive success focusing on whether nest predation is higher in invaded relative to un-invaded communities.

Methods

Artificial nests

To determine whether Argentine ants recruit to bird eggs more than the native species they displace, we placed ten nests each 1) in areas invaded by Argentine ants, 2) at the front of the invasion where Argentine ants and native ants co-occurred, and 3) in areas where the Argentine ant has not yet reached at the University of California's Elliot Chaparral Reserve. The reserve consists primarily of chemise chaparral vegetation and is nested within a larger area of undeveloped scrub-land (9254.5 ha). Argentine ants are invading the reserve from an adjacent developed area dominated by introduced *Eucalyptus* trees. Nests consisted of small baskets of interwoven twigs that mimicked natural birds nests and were attached directly to vegetation .5 to 1.5 meters off the ground. All nests were placed at least thirty meters apart, contained two quail eggs, and were covered with 1-cm wide hardware cloth to prevent other predators from reaching the eggs. We monitored nests every morning for ten days. At 0800 on the tenth day, a small 0.5 cm hole was poked into one egg to simulate a pipping chick. We then monitored the nests every hour to determine the recruitment rate of ants to the eggs. Differences in the number of nests recruited to by ants in invaded and uninvaded areas were examined using a chi-square test. Differences in recruitment rates between native and Argentine ants were examined with an ANOVA.

Dark-eyed Junco nests

To examine whether Argentine ants can cause nest failure in natural nests, we located nests of a ground nesting passerine, the Dark-eyed Junco, in an area invaded by Argentine ants, the campus of the University of California San Diego in La Jolla. This population of juncos has only recently become established in La Jolla and is the subject of a long-term evolutionary study (Yeh, 2004). Nests were located between February and August in 1998 2000 and were monitored three times a week. We attributed a predation event to *L. humile* if ants were swarming over nestlings that were still living (and later died) or if ants were eating nestlings that were alive the previous visit.

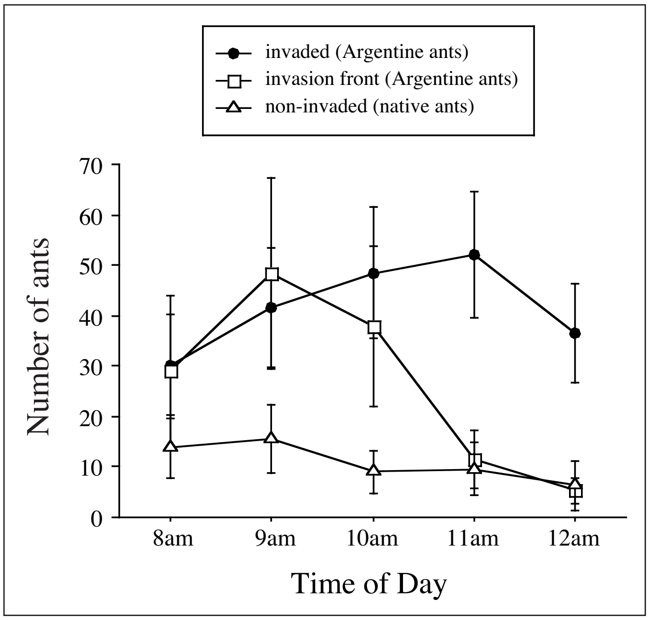

Fig. 1. Recruitment rates of the invasive Argentine ant and native ants to artificial bird nests baited with quail eggs. Symbols represent the mean (+1 s.e.) number of workers seen on the eggs at one-hour intervals after a small hole was made to simulate a pipping chick. The Argentine ant was the only species to recruit to nests placed in invaded areas and at the front of the invasion.

Results

Artificial nests

Argentine ants were seen foraging on the eggs in 8 of 20 nests placed in occupied areas while native species of ants recruited to only 4 of 20 nests in areas at the front of the invasion or without the Argentine ant. Daily examination of the eggs revealed no evidence that either Argentine ants or native ants were causing damage to the eggs. When a small (0.5 cm) hole was made in one egg to simulate a pipping chick, Argentine ants recruited to more nests than native ants (Argentine ants: 9 of 10 nests in invaded areas and 6 of 10 nests at the invasion front; native ants: 0 nests at the invasion front and 4 of 10 nests in un-invaded areas) (invaded vs un-invaded sites: $df = 1$, $X^2 = 5.49$, $p = 0.019$). After 4 hours, Argentine ants also recruited in higher numbers to artificial eggs than native ants but only in the invaded site (df = 2,27, F = 7.484, p = 0.0026; Fisher's PLSD: invaded vs un-invaded $p = 0.0028$, invaded vs invasion front $p = 0.0021$, invasion front vs un-invaded $p = .9139$) (Fig. 1). Only two species of native ants recruited to the eggs, *Forelius mccooki* (1 nest) and *Tapinoma sessile* (4 nests). *Tapinoma sessile*, like the Argentine ant, has very mobile colonies and will frequently forage on vegetation.

Dark-eyed Junco nests

We found 403 dark-eyed junco nests over three years, 334 (83 %) of which contained eggs. Of these, 87 (26 %) nests failed before hatching (preyed upon or abandoned), however, none obviously the result of ant harassment or predation. Of 247 nests that made it to the nestling phase, 59 (24 %) were preyed upon but only 4 (<2 %) appeared to fail as a direct result of recruitment by Argentine ants. Predation by vertebrates appeared to be the largest component of nest failure accounting for 56 % of losses during incubation and 82 % of losses during the nestling phase. For nests reaching at least the egg stage, overall sources of nest failure ranked as follows: vertebrate predation (31 %), abandonment (11 %), cowbird (*Molothrus ater*) brood parasitism (3 %), and Argentine ant predation (1 %).

Discussion

It has been suggested that ant invasions are causing the decline of many vertebrates, especially ground-nesting birds (Allen et al., 1994). Two mechanisms have been invoked: the direct predation of nests and an indirect impact through a reduction of available resources. Our artificial nest experiments suggest that *L. humile* locate and recruit to more eggs than native ant species. The ability of Argentine ants to excel at both interference and exploitative competition is linked to the high densities they achieve in invaded areas (Human and Gordon, 1996; Holway, 1999) and may be responsible for the success of invasive ants generally (Holway et al., 2002). The monitoring of dark-eyed junco nests also provides direct evidence that Argentine ants can cause nest failure. However, overall rates of failure due to Argentine ants were low compared to other factors. These results also serve as a reminder that data from artificial nests, although valuable for comparative purposes, may not emulate actual nesting success in many systems (Wilson et al., 1998).

Table 1. Impacts of the invasive Argentine ant (*Linepithema humile*) and red-imported fire ant (*Solenopsis invicta*) on avian nest mortality. For comparison, the impact of some native species of fire ants on avian nesting success are also shown.

Species impacted	Ant species	Location	Study Design[1]	Sample Size[2]	% Mortality[3]	% Reduction[4]	Reference
California gnatcatcher (*Polioptila melanura*)	*L. humile*	CA, USA	?	171	1.2	na	Sockman, 1997
Darked-eyed junco (*Junco hyemalus*)	*L. humile*	CA, USA	C	334	0.8–2.4	na	this paper
Least tern (*Sterna antillarum*)	*L. humile*	CA, USA	na	1 observation	na	na	Hooper, 1995 (p.142)
Dark-rumped petrel (*Pterodroma phaeopygia*)	*L. humile*	HI, USA	A	126	?	0.0	Krushelnicky et al., 2001
Least tern (*Sterna antillarum*)	*S. invicta*	MS, USA	B	?	25–45	26.7	Lockley, 1995
Colonial waterbirds[5]	*S. invicta*	TX, USA	B	40	67.0–100	92.0	Drees, 1994
Crested caracara (*Caracara plancus*)	*S. invicta*	TX, USA	C	7	28.5	na	Dickinson, 1995
Northern bobwhite (*Colinus virginianus*)	*S. invicta*	TX, USA	B	43	52.0	30.0	Mueller et al., 1999
Cliff swallow (*Hirundo pyrrhonota*)	*S. invicta*	TX, USA	A	1100	40.5	34.4	Sikes and Arnold, 1986
Barn swallow (*Hirundo rustica*)	*S. invicta*	TX, USA	C	178	11.8	na	Kopachena et al., 2000[6]
Black rail (*Laterallus jamaicensis*)	*S. invicta*	FL, USA	C	19	5.3	na	Legare and Eddleman, 2001
Wood duck (*Aix sponsa*)	*S. invicta*	TX, USA	C	20	15.0	na	Ridlehuber, 1982
Black-capped vireo (*Vireo atricapillus*)	*S. invicta*	TX, USA	C	142	10.6	na	Stake and Cimprich. 2003
Barn swallows (*Hirundo rustica*)	*S. geminata*	TX, USA	C	>25	4.0	na	Kroll et al., 1973
Quail	*S. geminata*?	FL, USA	na	2456	3.7–12.2	na	Travis, 1938
California quail (*Callipepla californica*)	*S. xyloni*	CA, USA	na	1 observation	na	na	Emlen, 1938
Black-bellied whistling duck (*Dendrocygna autumnalis*)	*S. xyloni*	TX, USA	na	1 observation	na	na	Delnicki and Bolen, 1977

na = not applicable (study design does not provide this information)
? = indicates that the information was not accessible from the paper
[1] Study design: A (compared infested to un-infested areas), B (compared untreated areas with areas treated with pesticides to control ants), C (only infested areas examined). A question mark is used for Sockman (1997) because it is not clear if the entire area of the study was occupied with Argentine ants.
[2] Number of nests found throughout the study (across all treatments/areas if applicable)
[3] Percent of nests that failed as a result of ant predation in infested areas. When nest success was examined over many time periods (months for Lockley, 1995 and Drees, 1994, years for Travis, 1938), the range is given.
[4] Percent reduction in nesting success in ant infested areas relative to un-infested or treated areas.
[5] Great Egret (*Casmerodius albus*), Great Blue Heron (*Ardea herodis*), Snowy Egret (*Egretta thula*), Roseate Spoonbill (*Ajaia ajaja*), Tricolored Heron (*Hydranassa tricolor*), Olivaceous Cormorant (*Phalacrorox olivaceus*), and Laughing Gull (*Larus atricilla*). Only data from 1991 of this study is presented here.
[6] In this study, barn swallows were studied in two areas, both infested with fire ants. One area had 24.7 % of nests depredated by red imported fire ants, the second area had no fire ant predation events despite that fire ants were almost 3 times as dense as in the first area. The data from both areas are used in this table.

In addition to directly causing chick mortality, Argentine ants may reduce resources for birds through the elimination of arthropod prey in areas where they have invaded. Like fire ants (Porter and Savignano, 1990), Argentine ants may negatively impact (reduce and disrupt) arthropod communities in areas where they have invaded (Cole et al., 1992; Human and Gordon, 1997; Bolger et al,. 2000; but see Holway, 1998). This change in arthropods, particularly native ants species, negatively affects species like the coastal horned lizard that forages primarily on ants (Suarez et al., 2000). Unlike many of the native ant species they displace, Argentine ants rarely disperse or eat seeds (Christian, 2001; Carney et al., 2003). The effect of invasive ants on granivorous birds remains unexplored.

In La Jolla, the entire nesting area of the Dark-eyed Junco is occupied by Argentine ants. We were therefore unable to compare nesting success in invaded areas to un-invaded areas. Given the low nest failure attributed to Argentine ants, such a comparison was unnecessary. However, it is possible that Argentine ants may influence nest success through mechanisms other than predation such as nest site placement or increased parental activity. If Argentine ants are reducing arthropod densities, adults may need to make more trips to and from the nest to provision their young. The presence of ant foragers in and around the nest may also cause parents to spend time removing ants at the expense of foraging. Increased parental activity around the nest may make the nest more visible to vertebrate predators. These indirect mechanisms of nest failure, particularly those relating to changes in parental behavior, remain largely unexplored.

A review of the literature reveals that nest failure rates attributed to invasive ants range from 0.8–2.4% of nests in areas invaded by *Linepithema humile* and 5.3–100.0% for *Solenopsis invicta* (Table 1). Relative to uninvaded or treated areas, this translates to a reduction in nesting success of between 26.7–92% in areas occupied by *S. invicta*. Relative to Argentine ants, ants in the genus *Solenopsis* may have stronger mandibles allowing them to penetrate eggshells (Hooper, 1995; Chalcraft and Andrews, 1999; but see Stake and Cimprich, 2003). Fire ants also possess a potent sting and can cause nest failure by directly killing chicks through repeated stinging. Red imported fire ant densities have been correlated with declines in northern bobwhite populations in eastern Texas (Allen et al., 1995) and exposure to as few as 50–200 *S. invicta* workers (for 60–15 seconds respectively) negatively affects the growth and survival of bobwhite chicks (Giuliano et al., 1996). Unlike *Solenopsis invicta*, Argentine ants do not sting and rely instead on spraying or smearing chemical defense compounds. However, they recruit to resources in extremely large numbers and may overwhelm their prey through suffocation, starvation by excluding feeding from the parents, or direct predation by repeated biting.
Future studies need to determine if the effects of invasive ants are greater than the impacts of the native species they displace. Many native species of ants may also be substantial egg or nestling predators. For example, *Solenopsis* (sub-genus Diploropthrum) ants are the main predators of *Anolis* eggs on Barro Colorado Island, Panama (Chalcraft and Andrews, 1999). Similarly, army ants in the tropics will take nearly anything that does not get out of the way during swarms including nestling birds (Robinson and Robinson, 2001). An important distinction needs to be made between the effects of non-native ants above and beyond the potential impacts that native species are already having. This is particularly true for ants in the genus *Solenopsis* as native fire ant species can be significant predators of bird nests (Emlen, 1938; Travis, 1938; Hooper, 1995).

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References

Allen C.R.,Demarais S. and Lutz R.S. 1994. Red imported fire ant impact on wildlife: an overview. *Texas J. of Science 46*: 51–59

Allen C.R., Lutz R.S. and Demarais S. 1995. Red imported fire ant impacts on Northern Bobwhite populations. *Ecol. Appl. 5*: 632–638

Allen C.R., Lutz R.S., Lockley T., Phillips Jr. S.A. and Demarais S. 2001. The nonindigenous ant, *Solenopsis invicta*, reduces loggerhead shrike and native insect abundance. *J. Agr. Urban Ent.18*: 249–259

Bolger D.T., Suarez A.V., Crooks K.R., Morrison S.A. and Case T.J. 1999. Effects of habitat fragmentation and Argentine ants on arthropods in southern California. *Ecol. Appl. 10*: 1230–1248

Carney S.E., Byerley M.B. and Holway D.A. 2003 Invasive Argentine ants (*Linepithema humile*) do not replace native ants as seed dispersers of *Dendromecon rigida* (Papaveraceae) in California, USA. *Oecologia 135*: 576–582

Chalcraft D.R. and Andrews R.M. 1999. Predation on lizard eggs by ants: Species interactions in a variable physical environment. *Oecologia 119*: 285–292

Christian C.E. 2001. Consequences of a biological invasion reveal the importance of mutualism for plant communities. *Nature 413*: 635–639

Cole F.R., Medeiros A.C., Loope L.L. and Zuehlke W.W. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology 73*: 1313–1322

Delnicky D.E. and Bolen E.G. 1997. Use of black-bellied whistling duck nest sites by other species. *Southwest. Nat. 22*: 275–277

Dickinson V.M. 1995. Red imported fire ant predation on Crested Caracara nestlings in south Texas. *Wilson Bull. 107*: 761–762

Drees B.M. 1994. Red imported fire ant predation on nestlings of colonial waterbirds. *Southwest. Ent. 19*: 355–359

Emlen J.T. Jr. 1938. Fire ants attacking California quail chicks. *Condor 40*: 85–86

Giuliano W.M., Allen C.R., Lutz R.S. and Demarais S. 1996. Effects of red imported fire ants on Northern Bobwhite chicks. *J. Wild. Manage. 60*: 309–313

Holway D.A. 1998. Effect of Argentine ant invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia 116*: 252–258

Holway D.A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology 80:* 238–251
Holway D.A., Lach L., Suarez A.V., Tsutsui N. and Case T.J. 2002. The ecological causes and consequences of ant invasions. *Ann. Rev. Ecol. Syst. 33*: 181–233
Hooper L.M. 1995. The biology of the southern fire ant, *Solenopsis xyloni*, (McCook) and its predation of the California least tern, *Sterna antillarum brownii* (Mearns). M.S. thesis. University of California, Riverside
Human K.G. and Gordon D.M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia 105*: 405–412
Human K.G. and Gordon D.M. 1997. Effects of Argentine ants on invertebrate biodiversity in northern California. *Con. Biol. 11*: 1242–1248
Kopachena J.G., Buckley A.J. and Potts G.A. 2000. Effects of the red imported fire ant (*Solenopsis invicta*) on reproductive success of barn swallows (*Hirundo rustica*) in northeast Texas. *Southwest. Nat. 45*: 477–482
Kroll J.C., Arnold K.A. and Gotie R.F. 1973. An observation of predation by native fire ants on nestling barn swallows. *Wilson Bulletin 85*: 478–479
Krushelnycky P.D., Hodges C.S.N., Medeiros A.C. and Loope L.L. 2001. Interaction between the Hawaiian dark-rumped petrel and the Argentine ant in Haleakala National Park, Maui, Hawaii. *Stud. Avian Biol. 22*: 243–246
Legare M.L. and Eddleman W.R. 2001. Home range size, nest-site selection and nesting success of Black Rails in Florida. *J. Field Ornith. 72*: 170–177
Lockley T.C. 1995. Effect of imported fire ant predation on a population of the least tern – an endangered species. *Southwest. Nat. 20*: 517–519
McGlynn T.P. 1999 The worldwide transfer of ants: geographical distribution and ecological invasions. *J. Biogeogr. 26*: 535–548
Parker I.M., Simberloff D., Lonsdale W.M., Goodell K., Wonham M., Kareiva P.M., Williamson M.H., Von Holle B., Moyle P.B., Byers J.E. and Goldwasser L. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biol. Invas. 1*: 3–19
Porter S.D. and Savignano D.A. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology 71*: 2095–2106
Ridlehuber K.T. 1982. Fire ant predation on wood duck ducklings and pipped eggs. *Southwest. Nat. 27*: 222
Robinson W.D. and Robinson T.R. 2001. Observations of predation events at bird nests in central Panama. *J. Field Ornith. 72*: 43–48
Robinson S.K., Thompson III F.R., Donovan T.M., Whitehead D.R. and Faaborg J. 1995. Regional effects of forest fragmentation on the nesting success of migratory birds. *Science 267*: 1987–1990
Sikes P.J. and Arnold K.A. 1986. Red imported fire ant (*Solenopsis invicta*) predation on cliff swallow (*Hirundo pyrrhonota*) nestlings in east-central Texas. *Southwest. Nat. 31*: 105–106
Sockman K.W. 1997. Variation in life-history traits and nest-site selection affects risk of nest predation in the California Gnatcatcher. *Auk 114*: 324–332
Stake M.M. and Cimprich D.A. 2003. Using video to monitor predation at black-capped vireo nests. *Condor 105*: 348–357
Suarez A.V. and Case T.J. 2002. Bottom-up effects on persistence of a specialist predator: ant invasions and horned lizards. *Ecol. Appl. 12*: 291–298
Suarez A.V., Bolger D.T. and Case T.J. 1998. Effects of fragmentation and invasion on native ant communities of coastal southern California. *Ecology 79*: 2041–2056
Suarez A.V., Richmond J.Q. and Case T.J. 2000. Prey selection in horned lizards following the invasion of the Argentine ant in southern California. *Ecol. Appl. 10*: 711–725
Suarez A.V., Holway D.A. and Case T.J. 2001. Patterns of spread in biological invasions dominated by long-distance jump dispersal: insights from Argentine ants. *Proc. Nat. Acad. Sci.* USA *98:* 1095–1100
Travis B.V. 1938. The fire ant (*Solenopsis* spp.) as a pest of quail. *J. Econ. Ent. 31*: 649–665
Wilson G.R., Brittingham M.C. and Goodrich L.J. 1998. How well do artificial bird nests estimate success of real nests? *Condor 100*: 357–364
Wojcik D.P., Allen C.R., Brenner R.J., Forys E.A., Jouvenaz D.P. and Lutz S.R. 2001. Red imported fire ants: Impact on biodiversity. *Am. Ent. 47*: 16–23