

A review of the introduced smooth-billed ani Crotophaga ani in Galápagos

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ABSTRACT

The smooth-billed ani (*Crotophaga ani*) is a widespread introduced bird species in the biologically important archipelago of Galápagos. Many scientists and local people consider it to be a damaging invasive, and it is possible that it impacts native species and ecosystems via multiple mechanisms. However, evidence for this is largely anecdotal and research on smooth-billed anis in Galápagos is limited. Despite this, there have been repeated attempts to control or eradicate the population over the past few decades, all without long-term success. These attempts continue, but no official plan of action regarding this species currently exists.

This review brings together all available information on smooth-billed anis in Galápagos. We use both published and unpublished research to answer the following questions:

- 1. What is known about the history of the smooth-billed anis' introduction to Galápagos?
- 2. What are the possible impacts of smooth-billed anis in Galápagos?
- 3. What attempts have been undertaken to control or eradicate smooth-billed anis in Galápagos and what were their outcomes?

In answering these questions, we highlight numerous knowledge gaps, in both the current understanding of the impacts of this introduced species and the effectiveness of potential control or eradication methods. We find an urgent need for further research before considered, resourceefficient decisions can be made regarding smooth-billed anis in Galápagos.

Keywords: Invasive species; alien bird species; island invasions; impacts of introduced species; control of introduced species; eradication

1 INTRODUCTION

Galápagos is a unique archipelago and one of the most pristine ecosystems in the world. It is a UNESCO World Heritage Site and has previously been identified as one of the 'most irreplaceable protected areas' in the world (Le Saout et al. 2013), a 'flagship' conservation area (González et al. 2008) and a Priority Ecoregion for Global Conservation (Olson & Dinerstein 2002). Ninety-seven percent of the terrestrial land (González et al. 2008) and 138,000 km² of the surrounding waters (Edgar et al. 2008) form the protected Galápagos National Park and Galápagos Marine Reserve respectively.

Unfortunately, despite their protection, these islands are under threat. The resident human population in Galápagos is over 25,000 (INEC 2015) and an approximate 200,000 tourists visit each year (Observatorio de Turismo de Galápagos 2018), leading to development pressures, issues of overfishing and pollution, and increased need for imported resources from continental South America (Izurieta et al. 2018). Both local human activities and climate change threaten native biodiversity in Galápagos, a high proportion of which is found nowhere else in the world (Tye et al. 2002). Introduced species, which have repeatedly arrived with the flow of people and resources being transported to the islands, have been identified as one of the major environmental issues for the archipelago (Izurieta et al. 2018).

Invasive species (i.e., introduced species that negatively impact their new environment) are among the greatest threats to biodiversity worldwide (Vitousek et al. 1997, IUCN 2000, Simberloff 2000,

Sala et al. 2000, CBD 2006, Clavero et al. 2009) and are considered a major driver of extinctions (Clavero & García-Berthou 2005). In island ecosystems, invasive species are often particularly damaging (Vitousek 1988). For example, in the Hawaiian Islands, they are implicated in the decline and extinction of many native species (Ziegler 2002), including plants (Vitousek & Walker 1989, Hughes & Vitousek 1993) and endemic birds (Scott et al. 1988, Athens et al. 2002, Reed et al. 2012). Often, management, control and eradication of invasive species involves significant economic costs and success can be difficult to attain (Howald et al. 2007, POST 2008, Williams et al. 2010).

To date, 1,579 species have been introduced to Galápagos, of which 1,476 have become established (Toral-Granda et al. 2017), including mammals, insects, fish, reptiles, amphibians, birds and plants. Many of these species have been declared as invasive, such as the parasitic fly (*Philornis downsi*) (Causton et al. 2006); the black rat (*Rattus rattus*) (Phillips et al. 2012); the feral dog (*Canis lupus familiaris*) (Phillips et al. 2012); and the blackberry (*Rubus niveus*) (Rentería et al. 2012a). Some larger vertebrates have already been successfully removed from some islands, such as feral donkeys (*Equus asinus*) (Carrión et al. 2007); feral pigs (*Sus scrofa*) (Cruz et al. 2005); and feral goats (*Capra hircus*) (Cruz et al. 2009), but at substantial monetary cost. Control or eradication programs are currently underway for several other species (Causton & Sevilla 2007, Jiménez-Uzcátegui & Zabala-Albizua 2008, Gardener et al. 2010, Phillips et al. 2012), with mixed success to date.

The smooth-billed ani (*Crotophaga ani*) (**Figure 1**), a member of the cuckoo family, is one of these introduced species in Galápagos. It is one of only three bird species to have become established in the archipelago, the others being cattle egrets (*Bubulcus ibis*), which could have arrived on the islands naturally, and feral chickens (*Gallus gallus*) (Phillips et al. 2012). Introductions of bird species worldwide are relatively uncommon compared to those of mammals and consequently have been studied less (Blackburn et al. 2009, Kumschick & Nentwig 2010, Strubbe et al. 2011). Their impact is a topic of debate (Kumschick & Nentwig 2010, Strubbe et al. 2011), but several species are thought, or have been shown, to be harmful nonetheless (Lowe et al. 2000, Brook et al. 2003, Smith et al. 2005, Pimentel et al. 2005, Linz et al. 2007, Strubbe & Matthysen 2007, Grarock et al. 2013, Feare et al. 2015). Shirley & Kark (2009) found habitat-generalist, multi-brooded species, which form large feeding or roosting flocks - all of which apply to smooth-billed anis (Loflin 1983, Quinn & Startek-Foote 2000) - to have the greatest impacts as introduced bird species.

The smooth-billed ani has a vast native range, from Argentina and Uruguay up to Florida, including most islands in the Caribbean (Quinn & Startek-Foote 2000, Birdlife International 2012). Individuals have also been recorded in other parts of North America, including Louisiana and Ohio (McLean et al. 1995, Remsen & Sweet 2008). They are found in a range of habitats (Giner & Strahl 1988, Beltzer et al. 2009) but typically do well in disturbed, human and agricultural areas (Souza 1995, Ridgely & Greenfield 2001a, Kennedy et al. 2010).

They have strikingly complex communication (Grieves et al. 2014, 2015) and breeding systems, with birds existing in large groups (typically numbering up to 25) in which all individuals build, use, and defend the same nest (Bent 1940, Davis 1940, Blanchard 2000, Quinn & Startek-Foote 2000, Schmaltz et al. 2008). They are territorial and will chase away and even kill individuals from other groups (Davis 1940, Loflin 1983).

Their diet is mainly insectivorous and herbivorous (Young 1929, Bent 1940, Skutch 1966, Tamayo 1981, Burger & Gochfeld 2001, Beltzer et al. 2009) and they are often found alongside cattle, feeding on the insects flushed by them (Young 1929, Rand 1953, Smith 1971, Ridgely & Greenfield 2001b, Restall et al. 2006). Some consider them beneficial in their native range due to their propensity to depredate agricultural pest insects (Colmenares Sifuentes & Fernandez-Badillo 1991), including ticks

(Koster 1971, Ridgely & Greenfield 2001b, Sazima 2008). However, they have also been suspected of, and in some cases proven to, kill and consume the occasional vertebrate including frogs (Young 1929, Koster 1971), lizards (Gill & Stokes 1971) and nestling and adult birds as well as eggs (Bent 1940, Haverschmidt 1955, Gill & Stokes 1971, Olivares & Munves 1973, Eitniear & Tapia 2000).

The biological importance of the archipelago, and the risks that introduced species so often present, mean it is vital that smooth-billed anis in Galápagos are monitored and their effects on native species and ecosystems understood. We reviewed all available research on smooth-billed anis in Galápagos to answer three main questions:

- 1. What is known about the history of the smooth-billed anis' introduction to Galápagos?
- 2. What are the possible impacts of smooth-billed anis in Galápagos?
- 3. What attempts have been undertaken to control or eradicate smooth-billed anis in Galápagos and what were their outcomes?

Answering these questions is a necessary first step towards deciding whether management of this species is a priority and, if so, what specific actions may be needed. Collating this information will also identify knowledge gaps vital to fill if such management decisions are to be properly informed.



Figure 1. A group of three smooth-billed anis in Galápagos (photo cred. Michael Dvorak)

2 METHODS

We obtained material for this review in 2016-2018, using the protocol outlined in **Figure 2**. The online search engines used were Google and Google Scholar and searches were done using the following search terms: "Smooth-billed ani"; "Crotophaga ani"; "Galápagos". The libraries visited were Harvard University Ernst Mayr Library; University of Hawai'i at Mānoa Hamilton Library; and Tufts University Tisch Library.

We also extracted observation records of smooth-billed anis in Galápagos from:

- 1. All works already obtained in the protocol outlined in Figure 2
- 2. Records collected by the Charles Darwin Foundation up until July 2018 (CDF unpubl. data)
- Records submitted to the Cornell Lab of Ornithology's eBird (Cornell Lab of Ornithology 2018) up until July 2018
- 4. Personal records from authors who were contacted directly



Figure 2. The protocol followed to obtain material for this review

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3 RESULTS

In total we located and analysed 99 works relating to smooth-billed anis and, where relevant, the closely related groove-billed ani (*Crotophaga sulcirostris*) (**Table 1**).

Material type	Number
Articles	59
Books	15
Datasets	1
Reports	15
Theses	7
Websites	2

Material source	Number
Authors	10
Charles Darwin	11
Foundation archives	
Libraries	10
Online	66
Universities	2

3.1 What is known about the history of the smooth-billed anis' introduction to Galápagos?

Smooth-billed anis are generally thought to have arrived in Galápagos in the 1960s (Rosenberg et al. 1990, Wiedenfeld 2006, Trueman et al. 2011, Connett et al. 2013). The first record was on Isabela in 1962 (Harris 1973, Grant & de Vries 1993, Tapia et al. 2000, Jiménez-Uzcátegui & Zabala-Albizua 2008), though there is a possibility that they were spotted as early as the 1950s (Jara 1995). They were originally identified as groove-billed anis (Harris 1973) but it is now believed that this was in error and that only smooth-billed anis ever reached Galápagos (Wiedenfeld 2006, Phillips et al. 2012).

Many scientists believe that smooth-billed anis (hereafter anis) did not arrive naturally to the islands but were brought over from continental South America by local farmers (Harris 1978, Ballestros 1983, Rosenberg et al. 1990, Grant & de Vries 1993). This view is also held by many local people and Galápagos National Park Directorate (hereafter GNPD) rangers (pers. comm.). In addition, the majority of farmers interviewed on Santa Cruz in the 1980s admitted that anis were deliberately introduced (Sandler 1988a). Three people were reportedly identified who may have brought anis over from the continent, but all denied responsibility (Ballestros 1983).

Farmers at the time believed anis fed upon ticks that parasitised cattle (Rosenberg 1987, Sandler 1988b, Rosenberg et al. 1990), hence their local name "garrapatero" meaning "tick-eater" (Jackson 1993). Reportedly, ticks were accidentally introduced to Galápagos in the early 1960s with cattle brought over to Isabela (Kastdalen 1982). Shortly after, the islands suffered a drought which, combined with what had become a heavy infestation of ticks, resulted in the deaths of large numbers of cattle (Kastdalen 1982). It follows that farmers would have been eager to find a way to deal with the ticks, which may have led to the anis' introduction (Harris 1973, 1978, Rosenberg 1987, Sandler 1988b, Rosenberg et al. 1990, Jackson 1993, Kricher 2002, Peters & Kleindorfer 2017). Unfortunately, although anis are often seen foraging amongst cattle in Galápagos (Castro & Phillips

1996, Swash & Still 2000), they do not appear to depredate ticks to any great extent, if at all (Rosenberg 1987, Sandler 1988b, Connett et al. 2013).

The means of their introduction has never been fully confirmed however and, while some believe anis are incapable of flying the 1000-km distance from the continent to Galápagos (Harris 1973, 1978, Sandler 1988b, Grant & de Vries 1993), the possibility of them having arrived naturally has been considered by some (Jara 1995). It has been argued, however, that, even if anis did reach the islands unaided, it is unlikely they would have been able to colonise them had the landscape not been already modified by humans for agriculture (Grant & de Vries 1993). Jara & de Vries (1995) commented that two of the first documented observations were in coastal, not farming areas, thus potentially contradicting this idea, but this conflicts with the earlier report by Harris (1973) stating that these observations in fact occurred inland.

Since their introduction, anis have been recorded on all eighteen main islands in Galápagos except Darwin (Figure 3; Table B.1) and the most recent population estimate was 250,000, of which 80,000 were on Santa Cruz (Connett et al. 2013). These counts were achieved using transects both on foot and by vehicle, with a fixed width of 200m, on Santa Cruz and extrapolated for the other islands known to have ani populations (V. Carrión - pers. comm.) Anis occur in most habitats across the islands (Robolino 1984, Jackson 1993, Castro & Phillips 1996, Luzuriaga et al. 2012) and have even been spotted on the largely inhospitable flanks of volcanos Wolf and Darwin on Isabela (CDF unpubl. data.). They have also been recorded on the smaller islands of Daphne Major (some records state only "Daphne" so it is possible anis have also been seen on Daphne Minor) and South Plaza, as well as Floreana's islets of Champion and Gardner-by-Floreana (Table B.1). As Isabela, Santa Cruz, San Cristóbal and Floreana – the four inhabited islands – have a history of agriculture (Lundh 2006), it is possible that they were introduced by humans to all of these, but it is unlikely their colonisation of any of the uninhabited islands was ever directly aided.

The expansion of the ani population in Galápagos has not been a steady rise but has seen several booms and crashes, seemingly coinciding with climatic changes (Phillips et al. 2012). Anis have appeared to benefit from El Niño years - they spread rapidly during the severe El Niños of 1982-83 and 1997-98 (Jackson 1985, Grant & Grant 1987, Sandler 1988b, Trillmich 1991, Castro & Phillips 1996, Snell & Rea 1999, Tapia et al. 2000, Vargas & Bensted-Smith 2000, Kricher 2002, Valle 2013). During periods of drought, populations appeared to decline, and anis have even temporarily disappeared from some smaller islands (Rosenberg 1988, Sandler 1988b, Wiedenfeld 2005). A severe drought in 1988 saw a decline of approximately 95% in the ani population on Santa Cruz (Sandler 1988b) (**Figure 4**). Several of the smaller islands have seen repeated cycles of ani die-out (or in some cases eradication) followed by re-colonisation (**Table B.1**).



Figure 3. Maps of Galápagos showing which islands had records of anis in each of the past six decades. Black indicates anis were recorded during that decade, white indicates no anis were recorded. Note that absence of a record does not mean absence of the species, as surveys were not completed on all islands each year. The northernmost islands Darwin and Wolf (situated in the black rectangle) have been moved south of their actual location for ease of view. The original records for each island are given in **Table B.1**.



Figure 4. Population estimates of smooth-billed anis on Santa Cruz (Ballestros 1983, Rosenberg 1987, Sandler 1988b, 1989, Rosenberg et al. 1990, Connett et al. 2013), showing the effect of the drought in 1988 and the population's subsequent and rapid recovery

3.2 What are the possible impacts of smooth-billed anis in Galápagos?

Limited research has been done on the impact of anis in Galápagos and large knowledge gaps have been highlighted previously by researchers (Fessl et al. 2010, Merlen 2013), but a variety of mechanisms by which they may be affecting native species and ecosystems has been suggested.

Predation

Dietary studies on anis in Galápagos have revealed similar results to those completed in their native range. They are predominantly herbivorous and insectivorous, and consume a range of invertebrates including Orthopterans, Lepidopterans, Hemipterans and Aranidans (Sandler 1988c, Rosenberg et al. 1990, Jara 1995, Tapia et al. 2000, Connett et al. 2013). Endemic invertebrate species depredated by anis include the Galápagos field cricket (*Gryllus abditus*) (Connett et al. 2013), Galápagos carpenter bee (*Xylocopa darwini*) (Sandler 1988c, Jara 1995, Connett et al. 2013), large painted locust (*Schistocerca melanocera*) (Rosenberg 1987, Connett et al. 2013) and Galápagos flightless grasshopper (*Halemus robustus*) (Connett et al. 2013). The high abundance of anis means it is possible they are having population-level impacts on some invertebrate species (Ballestros 1983, Phillips et al. 2012). Of particular concern is their depredation of Galápagos carpenter bees, the only native bee in the archipelago and an important pollinator (Chamorro et al. 2012).

As in their native range, anis have also been shown occasionally to take vertebrates in Galápagos. Several papers report ani depredation of endemic lava lizards (*Microlophus spp*) (Sandler 1988b, Jara 1995, Tapia et al. 2000, Connett et al. 2013). The finding of a Darwin's finch chick in the gizzard of an ani in 2009 (Connett et al. 2013) proves they will feed on endemic passerines, though it is possible the chick was already dead when found by the ani. However, anis have repeatedly been suspected of, and observed, robbing the nests of native bird species (Rosenberg 1987, Wiedenfeld & Jiménez-Uzcátegui 2008, O'Connor et al. 2010, Phillips et al. 2012), including Darwin's finches (specific species unconfirmed) (**Figure 5a**) (J. Lynton-Jenkins – pers. comm., Sandler 1988b, Jara & de Vries 1995), yellow warblers (*Setophaga petechia*) (Jara & de Vries 1995) and endemic mockingbirds (*Mimus spp.*) (Wiedenfeld 2005, GNPD rangers – pers. comm.). There have also been several observations of aggressive interactions between anis and adult mockingbirds (Rosenberg 1987, Rosenberg et al. 1990, Jara & de Vries 1995, Tapia et al. 2000), dark-billed cuckoos (*Coccyzus melacoryphus*) (Jara & de Vries 1995), finches (Jara & de Vries 1995, Tapia et al. 2000, O'Connor et al. 2010) and vermillion flycatchers (*Pyrocephalus rubinus*) (Jara & de Vries 1995), some of which resulted in the ani killing the other bird. These particular interactions might sometimes be a result of the anis' high degree of territoriality rather than direct predation.

It has been suggested that anis could threaten native passerine species in Galápagos on a population scale (Trillmich 1991, Peters & Kleindorfer 2017), including the vermillion flycatcher (Merlen 2013), the endemic and endangered Floreana (*Mimus trifasciatus*) and San Cristóbal (*Mimus melanotis*) mockingbirds (Rosenberg 1987, Llerena 2012) and the endemic and critically endangered mangrove finch (*Camarhynchus heliobates*) (Grant & Grant 1997, Vargas & Bensted-Smith 2000, Dvorak et al. 2004, Wiedenfeld 2005, Brumm et al. 2010, Fessl et al. 2010, Llerena 2012). However, there has been no research on the potential population-level impacts of occasional predation by anis on native bird species and, as suggested by Jara & de Vries (1995), their behaviour of nest robbing and attacking adult birds could be too rare to have any substantial impact.

Competition

The diet of the anis consists of many invertebrates that are eaten by native bird species and by lava lizards (*Microlophus albemariensis*), and it is possible that these species are suffering through resource competition (Rosenberg et al. 1990, Connett et al. 2013). However, no studies have directly investigated this.

Introduction and spread of other introduced species

Anis might also contribute to the spread of several introduced plant species (Guerrero & Tye 2011, Carrión-Tacuri et al. 2012). They are often found in areas dominated by invasive plants (Luzuriaga et al. 2012) and are known to feed on the fruits of many, including the tabasco pepper (*Capsicum frutescens*) (Guerrero & Tye 2011), the common guava (*Psidium guajava*) (Ballestros 1983), the wild-sage (*Lantana camara*) (Guerrero & Tye 2011, Connett et al. 2013), the currant tomato (*Solanum pimpinellifolium*) (Connett et al. 2013) and the blackberry (*Rubus niveus*) (Soria-Carvajal 2006, Guerrero & Tye 2011, Llerena 2012, Connett et al. 2013). Rather than crushing the seeds they eat, they often swallow and excrete them whole (Soria-Carvajal 2006, Guerrero & Tye 2011), increasing the possibility of them remaining viable after defaecation.

The anis' interaction with *R. niveus* is particularly concerning. It is a highly damaging species that has spread into multiple habitat types, displacing native vegetation (Rentería et al. 2012a). A study by Soria-Carvajal (2006) showed anis to be among the most common visitors to the plant and to remove more seeds than finch species that feed on *R. niveus*. Additionally, 57% of *R. niveus* seeds defaecated by anis were viable, far higher than the rates seen in finches. Other studies have shown endemic mockingbirds also to be important seed dispersers (Nogales et al. 2017) and effective distributors of *R. niveus* (Buddenhagen & Jewell 2006, Heleno et al. 2012), but their population densities in *R. niveus* prominent areas (the humid highlands including the agricultural zone and *Scalesia* forest (Rentería et al. 2012b, 2012a) are much lower (Dvorak et al. 2012, Luzuriaga et al. 2012).

Anis are also a host of the invasive parasitic fly *P. downsi*, in its native range as well as in Galápagos (Dodge & Aitken 1968, Fessl & Tebbich 2002, Causton et al. 2013). The invasion route of this parasite, which causes high chick mortality in many native bird species, is still unknown (Fessl et al.

2018). It has been suggested that *P. downsi* could have been introduced with anis (Kleindorfer & Sulloway 2016, Fessl et al. 2018), but no evidence for this has yet been found. It is, however, possible, given the body mass of the ani, that the species acts as a reservoir for *P. downsi*, without suffering itself, though studies to confirm this have not yet been undertaken.

Introduction and spread of disease and parasites

It is possible that novel diseases could have been introduced to Galápagos with the anis (Rosenberg et al. 1990) and continue to be spread by them. Additionally, they are hosts of both endo- and ectoparasites, in addition to *P. downsi* (Gottdenker et al. 2008), and could contribute to the spread of these amongst other avian species. However, very few studies on diseases in anis in Galápagos have been done (current knowledge on diseases in Galápagos is reviewed in (Bataille et al. 2018)).

Crop damage

It has been suggested by one researcher that anis may damage crops such as mandarin, orange and avocado by eating the fruits (Ballestros 1983) but no formal studies have been conducted.

Control of other introduced species

It is, however, possible that the presence of anis in Galápagos could be, in part, beneficial, due to their depredation of other introduced species. They have been recorded to prey upon introduced house mice (*Mus musculus*) (**Figure 5b**) (Connett et al. 2013), rats (specific species unknown) (Sandler 1988b, Llerena 2012), and various insects including the yellow paper wasp (*Polistes versicolour*) (Jara 1995, Llerena 2012), the Orthopteran *Copiphora brevicauda* (Connett et al. 2013), the Hemipterans *Anasa scorbutica* and *Nezara viridula* (Connett et al. 2013), the Australian cockroach (*Periplaneta australasie*) (Jara 1995) and the Surinam cockroach (*Pycnoscelis surinamensis*) (Jara 1995). However, there is no evidence that the populations of these species are significantly affected by ani predation.



Figure 5. a) A smooth-billed ani with a nestling it had just taken from a nest believed to be that of a small ground finch Geospiza fuliginosa, on Santa Cruz (photo cred. Joshua Lynton-Jenkins). b) A smooth-billed ani with an introduced mouse in its bill which it had caught alive and killed (photo cred. Luis Die Dejean, first published in Connett et al. 2013 and used here with permission of Galápagos Research)

3.3 What attempts have been undertaken to control or eradicate smooth-billed anis in Galápagos and what were their outcomes?

Many researchers consider smooth-billed anis to be a pest species in Galápagos and believe they should be controlled or eradicated (e.g. Ballestros 1983, Rosenberg 1987, Connett et al. 2013). Several GNPD rangers and local people also seem to be in agreement with this (pers. comm.). This has led to numerous attempts by the GNPD and the Charles Darwin Foundation (hereafter CDF) to control the population, but the success of these has been limited.

In 1986, 24 years after their estimated introduction to the islands, it was reported that anis had been eradicated from Santa Fé (Rosenberg 1988, Castro & Phillips 1996), supposedly by shooting. In early 1988, the GNPD and CDF began an intensive eradication program (Sandler 1988b) but it proved too costly and difficult to implement fully. Anis were quick to become wary of the shooters and dense vegetation cover meant a clear aim was hard to obtain (Sandler 1988b, 1988d). The biggest success of this program was on Pinzón, which had an ani population of only twelve individuals. Rather than hunt them during the day, the researchers sought out their night-time roost site. They managed to shoot six of the anis there and, unexpectedly, six were depredated by short-eared owls (*Asio flammeus*), whose population on the island had recently increased, reportedly due to a high number of rats (Rosenberg 1988, Sandler 1988b, 1988e, Castro & Phillips 1996).

New methods were then developed which involved recording the calls of anis from a particular group and playing them within range of another group. The hope was that the calls would elicit a territorial response, but this was not observed (Sandler 1988b, 1988c). It was then decided to test traps with live, wild-caught birds used as lures, again in the hope of inducing an attack on the 'intruding' bird, but this work was halted by a drought-induced crash in the ani population (Sandler 1988b). Additionally, the researchers faced difficulties keeping wild-caught lure birds alive in captivity (Sandler 1988c). Trapping with a lure had previously been used successfully in Costa Rica for the closely related groove-billed ani (Vehrencamp 1978, Vehrencamp et al. 1986, Bowen et al. 1989), although the results had been variable (Sandler 1988b). In addition, it was thought that trapping could be cheaper than shooting in areas of high ani population density. As they were declining rapidly at that time, efforts to develop an efficient method of trapping did not continue.

By 1989, however, the population had grown once more, and control efforts had begun again. A reported 898 anis were killed in the agricultural zone of Santa Cruz over the course of eight months (Jara & de Vries 1995). A record of the methods used for this has not been found but shooting anis at their night-time roost sites was suggested at an earlier planning stage (Sandler 1989). By 1990, the small, localised population of anis on Floreana had apparently been eliminated (Jara & de Vries 1995). Unfortunately, by 1991, anis had been reported again on Santa Fé, Pinzón and Floreana (**Table B.1**) (Rosenberg et al. 1990, Jara & de Vries 1995).

By 1993 anis were once again considered "common" (Jackson 1993) on Santa Cruz. In 1995 a student attempted to remove anis from two lowland areas on Isabela, by shooting them at their roost and foraging sites, but was only able to kill some of the birds seen, and at a slow rate (one every 80-95 minutes). They reported that shooting became more difficult over time, again due to the birds learning to fear the noise and becoming wary of shooters (Jara 1995, Jara & de Vries 1995), and that the dense vegetation was problematic. As a result, they felt that shooting would only work if entire groups could be eliminated at once.

The same student also tried trapping, using a live two-month old ani, a taxidermied adult ani and a live adult ani in turn (it is assumed that these lure birds were from a different group than those from

which a response was hoping to be elicited) (Jara 1995, Jara & de Vries 1995). Anis only showed interest when the live adult lure was used, and none of the birds ever entered the trap. Finally, the student tried mistnetting in combination with playback of recorded ani calls but discovered that anis were capable of recognising and avoiding the mistnets. They reported that both Beach (1990) and Palacios (1990b) had similar trouble catching anis with mistnets, but it was not possible to obtain these two papers for this review. They concluded that both traps and nets were unsuitable for catching large numbers of birds, due to the limited success seen and the requirement of a permanent human observer (Jara 1995, Jara & de Vries 1995). However, in the early 2000s, Schmaltz et al. successfully used both traps and mist nets to capture smooth-billed anis in Puerto Rico (Schmaltz et al. 2008).

After 1995, sporadic eradication attempts continued in Galápagos, and Castro and Phillips stated in 1996 that anis had been once again eradicated from Santa Fé and Pinzón (Castro & Phillips 1996). Shortly after, they were reported to have recolonised both islands during their range expansion in the 1997-98 El Niño (**Table B.1**) (Phillips et al. 2012). However, the original reference provided in the publication (Vargas & Bensted-Smith 2000) does not report this. Regardless, there have been other records of anis on both islands since 1996 (Merlen 2013, Cornell Lab of Ornithology 2018). The CDF successfully eradicated anis in one area of Isabela as part of a mangrove finch project in 1996-1998 (Vargas & Bensted-Smith 2000). It is unclear how long it took anis to recolonise this area, but they were reported there ten years later (CDF unpubl. data).

Patry (2002) reports the existence of eradication programs for anis on Fernandina, Marchena and Pinta in 2002. Phillips et al. (2012) state the Fernandina program as being successful but, along with Jiménez-Uzcátegui & Zabala-Albizua (2008) and Wiedenfeld (2006), state that the results from Marchena were not known. Anis also seemed to disappear from Genovesa in the early 2000s, but it is unclear whether this was due to an eradication program or natural causes (Patry 2002, Phillips et al. 2012). In the past decade there have been occasional records of anis on Fernandina and Genovesa (Cornell Lab of Ornithology 2018), but whether they are actually established there is currently unclear. Anis were reported again on Marchena in 2017 and on Pinta in 2018 (**Table B.1**) (CDF unpubl. data).

In 2009 the GNPD undertook a pilot study for ani eradication on Santa Cruz (Connett et al. 2013) but the outcome of this is not known. More recently, in 2012, a project was proposed to identify the most effective control method for anis, but the researchers were unable to complete the work due to issues obtaining licenses for firearms (Llerena 2012). Since then, the GNPD have continued sporadic control of anis by shooting, and occasional traps have been tried without success (GNPD rangers - pers. comm.).

Negative impacts of shooting attempts have not yet been investigated but it is possible that they may be causing disturbance to other species (Evans & Day 2002). In addition, the lead pellets usually used by the GNPD may be causing damage through contamination of the environment (Scheuhammer & Norris 1996, Cao et al. 2003) or ingestion by other species (Kendall et al. 1996, Fisher et al. 2006, Gangoso 2009, Neumann 2009, Pain 2009), such as Galápagos hawks (*Buteo galapagoensis*), which are known to scavenge (Rivera 2010).

As of yet, an efficient method of controlling or eradicating ani populations in Galápagos has not been identified and the cost and feasibility of such a program is a concern for several researchers (e.g. Sandler 1988a, 1988b, Jara & de Vries 1995).

4 CONCLUSIONS AND FUTURE DIRECTIONS

Galápagos is important to conservation for many reasons. It supports a wide range of native and endemic species and played a critical role in informing Charles Darwin's theory of evolution by natural selection. Unfortunately, many threats are facing this archipelago, one of which is the large number of non-native species introduced by humans. Although some of these are the current subjects of scientific investigation, others have not yet been sufficiently studied and could be having severe impacts.

The smooth-billed ani is one of these species. The current population is large and wide-ranging, and several mechanisms have been proposed by which they may be affecting native species and ecosystems, including predation, competition and dispersal of invasive plants and parasites. They are considered a pest by local people and GNPD rangers and a damaging invasive species by many scientists. Of particular concern to many is their behaviour of killing endemic birds and robbing their nests, and their contribution to the spread of the invasive plant *R. niveus*.

While these concerns are justified, research into anis in Galápagos has so far been limited and, as of yet, there is insufficient evidence of their impacts having any effect on a significant scale, nor has an effective method of control or eradication been identified. Despite this, there have been, and continue to be, repeated attempts to reduce the ani population, which have lacked long term success, are costly and are possibly causing conservation issues of their own. As there is a high number of introduced species in Galápagos, and limited resources with which to deal with them, it is important that focus be placed on establishing and prioritising those that need the most urgent attention and that control or eradication attempts be properly planned.

To this end, it is of urgent necessity that the impacts of anis in Galápagos be researched further. A wide-scale dietary analysis should be undertaken to determine the extent to which anis are depredating native and endemic vertebrates, as well as other introduced species. Studies of passerine and mockingbird breeding success in areas of differing density of anis and studies of the impact of anis on Galápagos carpenter bee populations would also be beneficial, as well as further study into their function as disease and parasite hosts and vectors.

Research into effective methods of control and eradication is also required, as highlighted by many other scientists (e.g. Sandler 1988c, Rosenberg et al. 1990, Dvorak et al. 2004, Llerena 2012). If eradication or further control is attempted, a wide-scale, resource-efficient plan will be needed to implement such methods. As anis are clearly able to rapidly recolonise islands after eradication, removing them from one island at a time would not suffice. In order to maximise possibilities of success, an evidence-based methodology should be used (Sutherland et al. 2004), with methods and results from prior control and eradication attempts of introduced species on islands globally being taken into consideration. It will be necessary to determine in advance whether the culling rate resulting from any control or eradication method could exceed the maximum growth rate of the population and whether the methods will still be effective as the population modelling (Dye 1984, McCarthy et al. 2013) to establish, for example, how many individuals would need to be culled in order to sufficiently affect populations on different islands. In addition, the support of local people for ani eradication, which is currently thought to be quite high, should be maintained to increase chances of success (Bomford & O'Brien 1995).

The biology of anis should also be used to inform control or eradication attempts. For example, trapping methods using playback could be refined using recent research on the vocalizations of anis

(Grieves et al. 2015). Additionally, as ani numbers in Galápagos typically decline during droughts, carrying out control and eradication efforts during drier years could achieve the best results (Sandler 1988b).

If control or eradication of anis is attempted, it will be important to ensure this runs in tandem with equivalent plans for introduced plants anis may be dispersing and other introduced species they may currently be controlling. Additionally, it should be noted that conservation of the Galápagos hawk and short-eared owl populations could prove beneficial in controlling ani populations as both species are known to depredate them (Sandler 1988b, B. Fessl pers. obs.).

The resource and economic cost of control and eradication programs, along with their potential to cause suffering to targeted individuals, disturb other wildlife and pollute ecosystems, means it is vital they are only attempted when known to be a priority, have a good chance of being successful in the long term, and when they are properly researched and planned. Before further control of smooth-billed anis is attempted in Galápagos, more research into the impacts they are having, as well as efficient methods of control or eradication, is required. However, due to the time this research will take, more immediate control of anis in areas in need of special and urgent preservation such as the habitat of the critically endangered mangrove finch, or areas where control of *R. niveus* is being undertaken, could be of benefit, if properly planned and carefully executed.

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REFERENCES

Athens, J. S., H. D. Toggle, J. V. Ward, and D. J. Welch. 2002. Avifaunal extinctions, vegetation change, and Polynesian impacts in prehistoric Hawai'i. Archaeology in Oceania **37**:57–78.

*°Ballestros, N. A. 1983. Los Garrapateros en la Parte Alta de la Isla Santa Cruz. Colegio Nacional Galápagos, Galápagos, Ecuador.

Bataille, A., I. I. Levin, and E. H. R. Sari. 2018. Colonization of parasites and vectors. Page Disease ecology: Galápagos birds and their parasites. Springer Science+Business Media, New York, NY.

Beltzer, A. H., M. A. Quiroga, C. F. Reales, and V. G. Alessio. 2009. Espectro trófico, ritmo circadiano de actividad alimentaria y uso del hábitat del pirincho negro Crotophaga Ani (Aves: Cuculidae) en el valle de inundación del Río Paraná Medio, Argentina. FABICIB **13**.

Bent, A. C. 1940. Life Histories of North American [birds]: Cuckoos, Goatsuckers, Hummingbirds and their allies. US Government Printing Office, Washington.

Birdlife International. 2012. Crotophaga.

Blackburn, T. M., J. L. Lockwood, and P. Cassey. 2009. Avian Invasions: The Ecology and Evolution of Exotic Birds. Oxford University Press.

Blanchard, L. 2000. An investigation of the communal breeding system of the Smooth-billed Ani (Crotophaga ani). McMaster University, Hamilton, Ontario.

Bomford, M., and P. O'Brien. 1995. Eradication or Control for Vertebrate Pests? Wildlife Society Bulletin (1973-2006) **23**:249–255.

Bowen, B. S., R. R. Koford, and S. L. Vehrencamp. 1989. Dispersal in the communally breeding Groove-Billed Ani (Crotophaga sulcirostris). The Condor **91**:52–64.

Brook, B. W., N. S. Sodhi, M. C. K. Soh, and H. C. Lim. 2003. Abundance and Projected Control of Invasive House Crows in Singapore. The Journal of Wildlife Management **67**:808–817.

Brumm, H., H. Farrington, K. Petren, and B. Fessl. 2010. Evolutionary dead end in the Galápagos: divergence of sexual signals in the rarest of Darwin's finches. PLoS ONE **5**:e11191.

Buddenhagen, C. E., and K. J. Jewell. 2006. Invasive plant seed viability after processing by some endemic Galápagos birds. Ornitología Neotropical **17**:73–80.

Burger, J., and M. Gochfeld. 2001. Smooth-billed ani (Crotophaga ani) predation on butterflies in Mato Grosso, Brazil: risk decreases with increased group size. Behavioral Ecology and Sociobiology **49**:482–492.

Cao, X., L. Q. Ma, M. Chen, D. W. Hardison, and W. G. Harris. 2003. Weathering of Lead Bullets and Their Environmental Effects at Outdoor Shooting Ranges. Journal of Environmental Quality **32**:526–534.

Carrión, V., C. J. Donlan, K. Campbell, C. Lavoie, and F. Cruz. 2007. Feral donkey (Equus asinus) eradications in the Galápagos. Biodiversity and Conservation **16**:437–445.

Carrión-Tacuri, J., R. Berjano, G. Guerrero, E. Figueroa, A. Tye, and J. M. Castillo. 2012. Predation on Seeds of Invasive Lantana camara by Darwin's Finches in the Galápagos Islands. The Wilson Journal of Ornithology **124**:338–344.

**Castro, I., and A. Phillips. 1996. A guide to birds of the Galápagos Islands. First edition. Princeton University Press, Princeton, New Jersey, USA.

Causton, C., F. Cunninghame, and W. Tapia. 2013. Management of the avian parasite Philornis downsi in the Galápagos Islands: A collaborative and strategic action plan. Galápagos Report **2011**–**2012**:167–173.

Causton, C. E., S. B. Peck, B. J. Sinclair, L. Roque-Albelo, C. J. Hodgson, and B. Landry. 2006. Alien Insects: Threats and Implications for Conservation of Galápagos Islands. Annals of the Entomological Society of America **99**:121–143.

Causton, C., and C. Sevilla. 2007. Latest records of introduced invertebrates in Galápagos and measures to control them:5.

CBD Secretariat of the Convention on Biological Diversity, 2006. Global Biodiversity Outlook 2.

Chamorro, S., R. Heleno, J. M. Olesen, C. K. McMullen, and A. Traveset. 2012. Pollination patterns and plant breeding systems in the Galápagos: a review. Annals of Botany **110**:1489–1501.

Clavero, M., L. Brotons, P. Pons, and D. Sol. 2009. Prominent role of invasive species in avian biodiversity loss. Biological Conservation **142**:2043–2049.

Clavero, M., and E. García-Berthou. 2005. Invasive species are a leading cause of animal extinctions. Trends in Ecology & Evolution **20**:110.

^AColmenares Sifuentes, S. B., and A. J. Fernandez-Badillo. 1991. Contribucion al conocimiento de la biologia y la ecologia de los Garrapateros, Crotophaga ani y C. sulcirostris en el valle del rio Guey.

*Connett, L., A. Guézou, H. W. Herrera, V. Carrión, P. G. Parker, and S. L. Deem. 2013. Gizzard contents of the smooth-billed ani Crotophaga ani in Santa Cruz, Galápagos Islands, Ecuador. Galápagos Research **68**.

*Cornell Lab of Ornithology. 2018. eBird Basic Dataset. Cornell Lab of Ornithology.

Cruz, F., V. Carrión, K. J. Campbell, C. Lavoie, and C. J. Donlan. 2009. Bio-Economics of Large-Scale Eradication of Feral Goats From Santiago Island, Galápagos. The Journal of Wildlife Management **73**:191–200.

Cruz, F., C. Josh Donlan, K. Campbell, and V. Carrión. 2005. Conservation action in the Galàpagos: feral pig (Sus scrofa) eradication from Santiago Island. Biological Conservation **121**:473–478.

*Curry, R. L., and S. H. Stoleson. 1988. New bird records from the Galápagos associated with the El Niño-Southern oscillation. The Condor **90**:505–507.

Davis, D. E. 1940. Social nesting habits of the Smooth-billed Ani. The Auk 57:179–218.

Dodge, H. R., and T. H. G. Aitken. 1968. Philornis Flies from Trinidad (Diptera: Muscidae). Journal of Kansas Entomological Society **41**:134–154.

*Dvorak, M., B. Fessl, E. Nemeth, S. Kleindorfer, and S. Tebbich. 2012. Distribution and abundance of Darwin's finches and other land birds on Santa Cruz Island, Galápagos: evidence for declining populations. Oryx **46**:78–86.

Dvorak, M., H. Vargas, B. Fessl, and S. Tebbich. 2004. On the verge of extinction: a survey of the mangrove finch Cactospiza heliobates and its habitat on the Galápagos Islands. Oryx **38**:171–179.

Dye, C. 1984. Models for the Population Dynamics of the Yellow Fever Mosquito, Aedes aegypti. Journal of Animal Ecology **53**:247–268.

Edgar, G. J., S. Banks, R. Bensted-Smith, M. Calvopiña, A. Chiriboga, L. E. Garske, S. Henderson, K. A. Miller, and S. Salazar. 2008. Conservation of threatened species in the Galápagos Marine Reserve through identification and protection of marine key biodiversity areas. Aquatic Conservation: Marine and Freshwater Ecosystems **18**:955–968.

Eitniear, J. C., and A. A. Tapia. 2000. Red-billed Pigeon (Columba Flavirostris) nest predated by Groove-billed Ani (Crotophaga sulcirostris). Ornitología Neotropical **11**:231–232.

Evans, D. M., and K. R. Day. 2002. Hunting disturbance on a large shallow lake: the effectiveness of waterfowl refuges. Ibis **144**:2–8.

Feare, C. J., C. Lebarbenchon, M. Dietrich, and C. S. Larose. 2015. Predation of seabird eggs by Common Mynas Acridotheres tristis on Bird Island, Seychelles, and its broader implications:10.

^aFessl, B., G. E. Heimpel, and C. E. Causton. 2018. Invasion of an avian nest parasite, Philornis downsi, to the Galápagos Islands: Colonization history, adapatations to novel ecosystems, and conservation challenges. Page Disease ecology: Galápagos birds and their parasites. Springer Science+Business Media, New York, NY.

Fessl, B., and S. Tebbich. 2002. Philornis downsi–a recently discovered parasite on the Galápagos archipelago–a threat for Darwin's finches? Ibis **144**:445–451.

Fessl, B., G. H. Young, R. P. Young, J. Rodriguez-Matamoros, M. Dvorak, S. Tebbich, and J. E. Fa. 2010. How to save the rarest Darwin's finch from extinction: the mangrove finch on Isabela Island. Philosophical Transactions of the Royal Society B: Biological Sciences **365**:1019–1030.

Fisher, I. J., D. J. Pain, and V. G. Thomas. 2006. A review of lead poisoning from ammunition sources in terrestrial birds. Biological Conservation **131**:421–432.

Gangoso, L. 2009. Long-Term Effects of Lead Poisoning on Bone Mineralization in Egyptian Vulture Neophron percnopterus. The Peregrine Fund.

Gardener, M. R., R. Atkinson, and J. L. Renteri-a. 2010. Eradications and people: lessons from the plant eradication program in Galápagos. Restoration Ecology **18**:20–29.

Gill, F. B., and C. C. Stokes. 1971. Predation on a netted bird by Smooth-billed Anis. The Wilson Bulletin **83**:101–102.

^DGiner, S., and S. D. Strahl. 1988. Segregacion de habtiat de tres especies simpatricas del genero Crotophaga. Universidad Central de Venezuela - Departamento de Biologia de Organismos.

González, J., C. Montes, J. Rodríguez, and W. Tapia. 2008. Rethinking the Galápagos Islands as a Complex Social-Ecological System: Implications for Conservation and Management. Ecology and Society **13**.

Gottdenker, N. L., T. Walsh, G. Jiménez-Uzcátegui, F. Betancourt, M. Cruz, C. Soos, R. E. Miller, and P. G. Parker. 2008. Causes of mortality of wild birds submitted to the Charles Darwin Research Station, Santa Cruz, Galápagos, Ecuador from 2002–2004. Journal of Wildlife Diseases **44**:1024–1031.

**Grant, P. R., and B. R. Grant. 1985. Responses of Darwin's finches to unusual rainfall. Pages 417– 447 in G. Robinson and E. M. del Pino, editors. El Nino in the Galápagos Islands: The 1982-1983 Event. First edition. Charles Darwin Foundation, Quito, Ecuador.

*Grant, P. R., and B. R. Grant. 1987. The extraordinary El Niño event of 1982-83: effects on Darwin's finches on Isla Genovesa, Galápagos. Oikos **49**:55.

*Grant, P. R., and B. R. Grant. 1997. The rarest of Darwin's finches. Conservation Biology **11**:119–126.

*Grant, P. R., and T. de Vries. 1993. The unnatural colonization of Galápagos by Smoothed-billed Anis (Crotophaga ani). Noticias de Galápagos **52**:21–23.

Grarock, K., D. B. Lindenmayer, J. T. Wood, and C. R. Tidemann. 2013. Does Human-Induced Habitat Modification Influence the Impact of Introduced Species? A Case Study on Cavity-Nesting by the Introduced Common Myna (<Emphasis Type="Italic">Acridotheres tristis</Emphasis>) and Two Australian Native Parrots. Environmental Management **52**:958–970.

Grieves, L. A., D. M. Logue, and J. S. Quinn. 2014. Joint-nesting smooth-billed anis, Crotophaga ani, use a functionally referential alarm call system. Animal Behaviour **89**:215–221.

Grieves, L. A., D. M. Logue, and J. S. Quinn. 2015. Vocal repertoire of cooperatively breeding Smoothbilled Anis. Journal of Field Ornithology **86**:130–143.

Guerrero, A. M., and A. Tye. 2011. Native and introduced birds of Galápagos as dispersers of native and introduced plants. Ornitol. Neotrop **22**:207–217.

*Harris, M. P. 1973. The Galápagos avifauna. The Condor 75:265–278.

**Harris, M. P. 1978. A field guide to the birds of Galápagos. William Collins Sons & Co Ltd, Glasgow, UK.

Haverschmidt, F. 1955. Notes on the life history of Todirostrum maculatum in Surinam. The Auk **72**:325–331.

Heleno, R. H., J. M. Olesen, M. Nogales, P. Vargas, and A. Traveset. 2012. Seed dispersal networks in the Galápagos and the consequences of alien plant invasions. Proceedings of the Royal Society B: Biological Sciences **280**:1–9.

Howald, G., C. J. Donlan, J. P. Galván, J. C. Russell, J. Parkes, A. Samaniego, Y. Wang, D. Veitch, P. Genovesi, M. Pascal, A. Saunders, and B. Tershy. 2007. Invasive Rodent Eradication on Islands. Conservation Biology **21**:1258–1268.

Hughes, F., and P. M. Vitousek. 1993. Barriers to Shrub Reestablishment following Fire in the Seasonal Submontane Zone of Hawai'i. Oecologia **93**:557–563.

INEC. 2015. Principales resultados Censo de Población y Vivienda Galápagos 2015.

IUCN. 2000. IUCN Guidelines for the Prevention of Biodiversity Loss Caused by Alien Invasive Species.

Izurieta, A., B. Delgado, N. Moity, M. Calvopiña, I. Cedeño, G. Banda-Cruz, E. Cruz, M. Aguas, F. Arroba, I. Astudillo, D. Bazurto, M. Soria, S. Banks, S. Bayas, S. Belli, R. Bermúdez, N. Boelling, J. Bolaños, M. Borbor, M. L. Brito, L. Bucheli, K. Campbell, D. Carranza, J. Carrión, M. Casafont, X. Castro, S. Chamorro, J. Chávez, D. Chicaiza, R. Chumbi, P. Couenberg, D. Cousseau, M. Cruz, N. d'Ozouville, C. de la Guía, G. de la Torre, C. M. Díaz, J. Duchicela, D. Endara, V. Garcia, C. Gellibert, J.

Gibbs, J. C. Guzmán, P. Heylings, A. Iglesias, J. C. Izurieta, P. Jaramillo, A. Klingman, A. Laurie, P. Leon, J. Medina, E. Mendieta, G. Merlen, C. Montalvo, E. Naula, D. Páez-Rosas, M. Peralta, M. Peralvo, M. Piu, J. Poma, J. Pontón, M. Pozo, D. Proaño, M. Ramos, A. Rousseaud, D. Rueda, P. Salinas, G. Salmoral, S. Saraguro, D. Simón-Baile, W. Tapia, B. Teran, M. Valverde, A. Vargas, J. Vega, W. Velásquez, A. Vélez, S. Verdesoto, H. G. Villarraga, F. Vissioli, C. Viteri-Mejía, L. Norris-Crespo, S. C. Cooke, M. V. Toral-Granda, and W. J. Sutherland. 2018. A collaboratively derived environmental research agenda for Galápagos. Pacific Conservation Biology **24**:168–177.

**Jackson, M. H. 1985. Galápagos: a natural history guide. First edition. The University of Calgary Press, Calgary, Alberta, Canada.

**Jackson, M. H. 1993. Galápagos: a natural history. Second edition. The University of Calgary Press, Calgary, Alberta, Canada.

*°Jara, M. E. 1995. Aspectos ecologico distribucion y abundancia del garrapatero en el sur de la isla Isabela, Galápagos. Pontificia Universidd Catolica del Ecuador, Quito, Ecuador.

*^oJara, M. E., and T. de Vries. 1995. Distribucion y abundancia del Garrapatero Crotophaga ani en las Islas Galápagos, Ecuador. Revista de la Pontificia Universidad Catolica del Ecuador 23:121–169.

*Jiménez-Uzcátegui, G., W. Llerena, W. B. Milstead, E. E. Lomas, and D. A. Wiedenfeld. 2011. Is the population of the Floreana mockingbird Mimus trifasciatus declining? Cotinga **33**:1–7.

*Jiménez-Uzcátegui, G., D. A. Wiedenfeld, F. H. Vargas, and H. L. Snell. 2015. CDF checklist of Galápagos birds. Charles Darwin Foundation.

*Jiménez-Uzcátegui, G., J. Zabala, B. Milstead, and H. L. Snell. 2012. CDF Checklist of Galápagos Introduced Vertebrates. Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador.

*Jiménez-Uzcátegui, G., and J. Zabala-Albizua. 2008. Status of introduced vertebrates in Galápagos. Galápagos Report **2006–2007**:136–141.

Kastdalen, A. 1982. Changes in the biology of Santa Cruz Island between 1935 and 1965. Noticias de Galápagos **35**:7–12.

Kendall, R. J., T. E. Lacker, C. Bunck, B. Daniel, C. Driver, C. E. Grue, F. Leighton, W. Stansley, P. G. Watanabe, and M. Whitworth. 1996. An ecological risk assessment of lead shot exposure in non-waterfowl avian species: Upland game birds and raptors. Environmental Toxicology and Chemistry **15**:4–20.

Kennedy, C. M., P. P. Marra, W. F. Fagan, and M. C. Neel. 2010. Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. Ecological Monographs **80**:651–669.

Kleindorfer, S., and F. J. Sulloway. 2016. Naris deformation in Darwin's finches: Experimental and historical evidence for a post-1960s arrival of the parasite Philornis downsi. Global Ecology and Conservation **7**:122–131.

^oKoster, F. 1971. Nesting behaviour of Ani, Crotophaga ani. Bonner Zoologische Beiträge **22**.

*Kricher, J. 2002. Galápagos. Smithsonian Institution, Washington, USA.

Kumschick, S., and W. Nentwig. 2010. Some alien birds have as severe an impact as the most effectual alien mammals in Europe. Biological Conservation **143**:2757–2762.

Le Saout, S., M. Hoffmann, Y. Shi, A. Hughes, C. Bernard, T. M. Brooks, B. Bertzky, S. H. M. Butchart, S. N. Stuart, T. Badman, and A. S. L. Rodrigues. 2013. Protected Areas and Effective Biodiversity Conservation. Science **342**:803–805.

Linz, G. M., H. J. Homan, S. M. Gaulker, L. B. Penry, and W. J. Bleier. 2007. European starlings: A review of an invasive species with far-reaching impacts:10.

^oLlerena, A. 2012. Measuring impact and optimizing control of the invasive smooth-billed ani in Galápagos, Ecuador. GNPS, GCREG, CDF and GC, Puerto Ayora, Galápagos, Ecuador.

^ALoflin, R. K. 1983. Communal behaviours of the Smooth-billed Ani. University of Miami, Miami, Florida.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species A selection from the Global Invasive Species Database.

Lundh, J. P. 2006. The farm area and cultivated plants on Santa Cruz, 1932-1965, with remarks on other parts of Galápagos:14.

Luzuriaga, N., F. Jiguet, M. Gardener, S. Veran, and P.-Y. Henry. 2012. Monitoring an endemic community of terrestrial birds: the Galápagos Islands Breeding Bird Survey (GIBBS). Bird Census News **25**:3–12.

McCarthy, R. J., S. H. Levine, and J. M. Reed. 2013. Estimation of effectiveness of three methods of feral cat population control by use of a simulation model. Journal of the American Veterinary Medical Association **243**:502–511.

McLean, E. B., A. M. White, and T. O. Matson. 1995. Brief note: Smooth-billed Ani (Crotophaga ani L.), a new Species of bird for Ohio. The Ohio Journal of Science **95**:335–336.

*Merlen, G. 2013. Gone, gone... going: the fate of the vermilion flycatcher on Darwin's islands. Galápagos Report **2011–2012**:180–184.

Neumann, K. 2009. Bald Eagle Lead Poisoning in Winter. The Peregrine Fund.

Nogales, M., A. González-Castro, B. Rumeu, A. Traveset, P. Vargas, P. Jaramillo, J. M. Olesen, and R. H. Heleno. 2017. Contribution by vertebrates to seed dispersal effectiveness in the Galápagos Islands: a community-wide approach. Ecology **98**:2049–2058.

O'Connor, J. A., R. Y. Dudaniec, and S. Kleindorfer. 2010. Parasite infestation and predation in Darwin's small ground finch: contrasting two elevational habitats between islands. Journal of Tropical Ecology **26**:285–292.

Olivares, A., and J. A. Munves. 1973. Predatory behaviour of Smooth-billed Ani. The Auk 90:891.

Olson, D. M., and E. Dinerstein. 2002. The Global 200: Priority Ecoregions for Global Conservation. Annals of the Missouri Botanical Garden **89**:199–224.

Observatorio de Turismo de Galápagos. 2018. www.observatorioGalápagos.gob.ec.

Pain, D. 2009. A Global Update of Lead Poisoning in Terrestrial Birds from Ammunition Sources. The Peregrine Fund.

*°Patry, M. 2002. Status of introduced vertebrates on the larger islands of the Galápagos and strategies for their management. Galápagos Report **2001–2002**:110–111.

*Peters, K. J., and S. Kleindorfer. 2017. Avian population trends in Scalesia forest on Floreana Island (2004-2013): Acoustical surveys cannot detect hybrids of Darwin's tree finches Camarhynchus spp. Bird Conservation International:1–17.

*Phillips, R. B., D. A. Wiedenfeld, and H. L. Snell. 2012. Current status of alien vertebrates in the Galápagos Islands: invasion history, distribution, and potential impacts. Biological Invasions **14**:461–480.

Pimentel, D., R. Zuniga, and D. Morrison. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics **52**:273–288.

POST Parliamentary Office of Science and Technology, 2008. Invasive non-native species. Postnote 303.

Quinn, J. S., and Startek-Foote. 2000. Smooth-billed Ani.

Rand, A. L. 1953. Factors affecting feeding rates of Anis. The Auk 70:26–30.

Reed, J. M., D. W. DesRochers, E. A. VanderWerf, and J. M. Scott. 2012. Long-Term Persistence of Hawaii's Endangered Avifauna through Conservation-Reliant Management. BioScience **62**:881–892.

Remsen, J. V., and P. Sweet. 2008. Discovery of a presumed-lost specimen of Smooth-billed Ani from Louisiana. North American Birds **62**:196–198.

Rentería, J. L., M. R. Gardener, F. D. Panetta, R. Atkinson, and M. J. Crawley. 2012a. Possible Impacts of the Invasive Plant Rubus niveus on the Native Vegetation of the Scalesia Forest in the Galápagos Islands. PLOS ONE **7**:e48106.

Rentería, J. L., M. R. Gardener, F. D. Panetta, and M. J. Crawley. 2012b. Management of the Invasive Hill Raspberry (Rubus niveus) on Santiago Island, Galápagos: Eradication or Indefinite Control? Invasive Plant Science and Management **5**:37–46.

⁺Restall, R., C. Rodner, and M. Lentino. 2006. Birds of Northern South America Vol 1. Christopher Helm, UK.

⁺Ridgely, R. S., and P. J. Greenfield. 2001a. The Birds of Ecuador; Status, Distribution and Taxonomy. Cornell University, Hong Kong.

⁺Ridgely, R. S., and P. J. Greenfield. 2001b. The Birds of Ecuador; Field Guide. Cornell University, Hong Kong.

Rivera, J. L. 2010. Galápagos Hawk: Demographic and Social Effects in a Changing Environment.

°Robolino, D. 1984. Estudio de campo del Garrapatero en Santa Cruz.

*°Rosenberg, D. K. 1987. Nuevas amenazas para las aves nativas. Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador.

* Rosenberg, D. K. 1988. Estado de los Garrapateros introducidos. Charles Darwin Foundation,
Puerto Ayora, Galápagos, Ecuador.

*Rosenberg, D. K., M. H. Wilson, and F. Cruz. 1990. The distribution and abundance of the smoothbilled ani Crotophaga ani (L.) in the Galápagos Islands, Ecuador. Biological Conservation **51**:113–123.

Sala, O. E., F. S. Chapin, Iii, J. J. Armesto, E. Berlow, J. Bloomfield, R. Dirzo, E. Huber-Sanwald, L. F. Huenneke, R. B. Jackson, A. Kinzig, R. Leemans, D. M. Lodge, H. A. Mooney, M. Oesterheld, N. L. Poff,

M. T. Sykes, B. H. Walker, M. Walker, and D. H. Wall. 2000. Global Biodiversity Scenarios for the Year 2100. Science **287**:1770–1774.

[©]Sandler, B. 1988a. Study of methodologies of eradication of the smooth billed ani in Galápagos. Charles Darwin Foundation, Galápagos, Ecuador.

*°Sandler, B. 1988b. History and present status of the introduced smooth-billed ani Crotophaga ani in Galápagos. Pages 104–106. Charles Darwin Foundation, Galápagos, Ecuador.

[©]Sandler, B. 1988c. Summary and conclusions of activities concerning smooth billed ani in Galápagos. Charles Darwin Foundation, Galápagos, Ecuador.

*[©]Sandler, B. 1988d. Eradication of Smooth-billed Ani Crotophaga ani Isla Pinzon. Charles Darwin Foundation, Galápagos, Ecuador.

*⁻Sandler, B. 1988e. Field trip itinerary report - Pinzon (October). Charles Darwin Foundation, Galápagos, Ecuador.

*⁻Sandler, B. 1988f. Field trip itinerary report - Pinzon (May). Charles Darwin Foundation, Galápagos, Ecuador.

*^CSandler, B. 1988g. Field trip itinerary report - Floreana (October). Charles Darwin Foundation, Galápagos, Ecuador.

*⁻Sandler, B. 1989. Proyectos de control y estudios de ecologia de garrapeteros. (Informe de Salida de Campo). Charles Darwin Foundation, Galápagos, Ecuador.

Sazima, I. 2008. Validated cleaner: the cuculid bird Crotophaga ani picks ticks and pecks at sores of capybaras in southeastern Brazil. Biota Neotropica **8**:213–216.

Scheuhammer, A. M., and S. L. Norris. 1996. The ecotoxicology of lead shot and lead fishing weights. Ecotoxicology **5**:279–295.

Schmaltz, G., J. S. Quinn, and C. Lentz. 2008. Competition and waste in the communally breeding smooth-billed ani: effects of group size on egg-laying behaviour. Animal Behaviour **76**:153–162.

Scott, J. M., C. B. Kepler, C. van Riper, and S. I. Fefer. 1988. Conservation of Hawaii's Vanishing Avifauna: Hawaiian Birds Provide One of the Best, and Most Spectacular, Showcases of Divergent Evolution. BioScience **38**:238–253.

Shirley, S. M., and S. Kark. 2009. The role of species traits and taxonomic patterns in alien bird impacts. Global Ecology and Biogeography **18**:450–459.

Simberloff, D. 2000. Nonindigenous Species - A Global Threat to Biodiversity and Stability. Page Nature and Human Society: The Quest for a Sustainable World. National Academies.

Skutch, A. F. 1966. Life history notes on three tropical American cuckoos. The Wilson Bulletin **78**:139–165.

Smith, G. C., I. S. Henderson, and P. A. Robertson. 2005. A model of ruddy duck Oxyura jamaicensis eradication for the UK. Journal of Applied Ecology **42**:546–555.

Smith, S. M. 1971. The relationship of grazing cattle to foraging rates in Anis. The Auk 88:876–880.

*Snell, H., and S. Rea. 1999. The 1997-98 El Niño in Galápagos: can 34 years of data estimate 120 years of pattern? Noticias de Galápagos **60**:111–20.

Soria-Carvajal, M. 2006. Avian seed dispersers of the invasive Rubus niveus (Rosaceae) in Santa Cruz Island, Galápagos, Ecuador. University of Missouri-St. Louis, Missouri, USA.

Souza, F. L. 1995. A study of group structure and home range size of Crotophaga ani and Guira guira in Sao Paulo, Brazil. Ararajuba **3**:72–74.

Strubbe, D., and E. Matthysen. 2007. Invasive ring-necked parakeets Psittacula krameri in Belgium: habitat selection and impact on native birds. Ecography **30**:578–588.

Strubbe, D., A. Shwartz, and F. Chiron. 2011. Concerns regarding the scientific evidence informing impact risk assessment and management recommendations for invasive birds. Biological Conservation **144**:2112–2118.

Sutherland, W. J., A. S. Pullin, P. M. Dolman, and T. M. Knight. 2004. The need for evidence-based conservation. Trends in Ecology & Evolution **19**:305–308.

**Swash, A., and R. Still. 2000. Birds, mammals & reptiles of the Galápagos Islands. Yale University Press, Connecticut, USA.

Tamayo, G. Y. 1981. Nota sobre la alimentacion del Garrapatero (Crotophaga ani) y su relacion cos ciertos cultivos. Memoria de la Sociedad de Ciencas Naturales La Salle:129–141.

*°Tapia, W., M. Patry, H. Snell, and V. Carrión. 2000. Estado actual de los vertebrados introducidos a las islas Galápagos. Informe Galápagos 1999–2000.

Toral-Granda, M. V., C. E. Causton, H. Jäger, M. Trueman, J. C. Izurieta, E. Araujo, M. Cruz, K. K. Zander, A. Izurieta, and S. T. Garnett. 2017. Alien species pathways to the Galápagos Islands, Ecuador. PLOS ONE **12**:e0184379.

**Trillmich, F. 1991. El Niño in the Galápagos Islands: a natural experiment. Pages 3–21 in H. A. Mooney, E. Medina, D. W. Schindler, E.-D. Schulze, and B. H. Walker, editors. Ecosystem Experiments. SCOPE, John Wiley & Sons Ltd, Chichester, West Sussex, UK.

*Trueman, M., L. Hannah, N. d'Ozouville, I. Larrea, and G. Di Carlo. 2011. Terrestrial ecosystems in Galápagos: potential responses to climate change. Pages 29–46 Climate change vulnerability assessment of the Galápagos islands. WWF & Conservation International, USA.

Tye, A., H. Snell, S. B. Peck, and H. Adsersen. 2002. Outstanding terrestrial features of the Galápagos archipelago. Page A Biodiversity vision for the Galápagos Islands. Charles Darwin Foundation and World Wildlife Fund, Puerto Ayora, Galápagos, Ecuador.

*Valle. 2013. Science and conservation in the Galápagos Islands. Pages 1–22 in S. J. Walsh and C. F. Mena, editors. Science and conservation in the Galápagos Islands: frameworks and perspectives. Springer, New York, USA.

*Vargas, H., and R. Bensted-Smith. 2000. Past and present ornithology in Galápagos. Bulletin de'l Institut Royal des Siences Naturalles de Belgique **70**:47–52.

Vehrencamp, S. L. 1978. The adaptive significance of communal nesting in Groove-Billed Anis (Crotophaga sulcirostris). Behavioral Ecology and Sociobiology **4**:1–33.

Vehrencamp, S. L., B. S. Bowen, and R. R. Koford. 1986. Breeding roles and pairing patterns within communal groups of groove-billed anis. Animal Behaviour **34**:347–366.

Vitousek, P. M. 1988. Diversity and Biological Invasions of Oceanic Islands. Page in E. O. Wilson and F. M. Peter, editors. Biodiversity. National Academies Press (US).

Vitousek, P. M., C. M. D'Antonio, L. L. Loope, M. Rejmanek, and R. Westbrooks. 1997. Introduced species: A significant component of human-caused global change. New Zealand Journal of Ecology **21**:1–16.

Vitousek, P. M., and L. R. Walker. 1989. Biological Invasion by Myrica Faya in Hawai'i: Plant Demography, Nitrogen Fixation, Ecosystem Effects. Ecological Monographs **59**:247–265.

*^oWiedenfeld, D. A. 2005. Censo de cucuves de Floreana 2005. Charles Darwin Foundation, Puerto Ayora, Galápagos, Ecuador.

*Wiedenfeld, D. A. 2006. Aves, the Galápagos Islands, Ecuador. Check List 2:1–27.

Wiedenfeld, D. A., and G. A. Jiménez-Uzcátegui. 2008. Critical problems for bird conservation in the Galápagos. Cotinga **29**:22–27.

Williams, F., Eschen, R., Harris, A., Djeddour, D., Pratt, C., Shaw, R. S., Varia, S., Lamontagne-Godwin, J., Thomas, S. E., Murphy, S. T. 2010. The economic cost of invasive non-native species on Great Britain.

WorldCat. 2017. www.worldcat.org.

Young, C. G. 1929. A Contribution to the Ornithology of the Coastland of British Guiana. Part II. Ibis:26–29.

Ziegler, A. C. 2002. Hawaiian Natural History, Ecology, and Evolution. University of Hawaii Press.

*Material used to produce **Table B.1** [°]Material sourced from CDF archives

- ^aMaterial sourced directly from an author
- ^AMaterial sourced directly from a university
- ⁺Material sourced from a library

Appendix A: Unobtainable Papers

The authors were unable to obtain the following works on smooth-billed anis in Galápagos, all of which were referenced in Jara 1995:

Anonymous, no date. Crotophaga ani: observations and census in Santa Cruz Island.

Beach, 1990. The smooth-billed ani: effects on native Galápagos landbirds, habitat use in nonagricultural area, and attraction experiments. Preliminary report.

Castro, 1989. Informe de viaje a la Isla Isabela.

Cruz & Sandler, 1988. Protection of native Galápagos ecosystems: The eradication of introduced species, the smooth billed ani, in the Galápagos Islands.

Harmon et al., 1984. Parasites of Anis in Galápagos. Propuesta.

Palacios, J., 1989. Analisis del contenido estomacal de 20 mollejas de /C. ani /colectadas en la zona Agricola de Santa Cruz en epoca de garua.

Palacios, J., 1990a. Analisis del contenido estomacal de 20 mollejas de /C. ani /colectadas en la zona Agricola de Santa Cruz en epoca de invierno.

Palacios, J., 1990b. Estudio de nido activo en la zona Agricola de Santa Cruz del 11 al 27 de enero.

Palacios, J., 1990c. Estudios de nidos activos de Crotophaga ani en la zona Agricola de Santa Cruz del 21 de enero al 30 de marzo.

Palacios, J., no date. Porque debemos erradicar a Crotophaga ani?

Reed and Bass, 1980. Census of smooth-billed anis in Santa Cruz.

Traimen et al., 1987. Census of smooth-billed ani.

Uribe, 1988. Estudio de garrapateros en Santa Cruz: Programacion de actividades para enero, febrero, y marzo de 1988.

Appendix B: Historical records of smooth-billed anis in Galápagos

Table B.1. Documented history of smooth-billed anis in Galápagos, including prior eradication attempts. *p* = recorded as present, *x* = recorded as not seen, *ER* = eradicated, blank = no information available. (¹This record refers to the early 1970s, the exact year is unknown; ²This observation was not confirmed; ³There is conflicting information for these two records. ⁴This record was just offshore of the island; ⁵There is confusion as to whether anis disappeared naturally here or were eradicated.) These observations were sourced from CDF unpublished data and personal observations (Grant & Grant unpubl. data; Sandler unpubl. data; Rosenberg unpubl. data) as well as articles, reports and datasets highlighted in the list of references for this paper.

	Baltra	Bartolomé	Champion	Daphnes	Española	Fernandina	Floreana	Gardner	Genovesa	Isabela	Marchena	North Seym	Pinta	Pinzón	South Plaza	Rábida	San Cristób	Santa Cruz	Santa Fé	Santiago	Wolf
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