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Wild-bird trade and exotic invasions: a new link of conservation concern?

Martina Carrete and José L Tella

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Wild-bird trade and exotic invasions: a new link of conservation concern?

Martina Carrete* and José L Tella

Exotic invasions are viewed as a major threat to global biodiversity, but predicting potential invaders is still a difficult task. Here, we highlight a hitherto unnoticed link between the increasing demand for pet birds in developed countries and avian invasions. Paradoxically, it is not the most common caged bird species that seem to be the most successful invaders, but those that are caught in the wild and traded on the pet market. Captive-bred species appear to have lost their ability to return to nature. Thus, the risk of biological invasion in importing countries should inform the current debate over potential bans on the wild-bird trade worldwide. This is a new piece of an already complex puzzle, in which the social, economic, and environmental aspects of both the importing and exporting countries must be weighed before any policy or resource-management measure can be instituted.

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Invasive species are considered to be one of the major threats to native biodiversity and ecosystem function, and their presence has social and economic implications worldwide (Wilcove *et al.* 1998; Kolar and Lodge 2001). Policies aimed at eradicating exotic invasives can be extremely costly (Myers *et al.* 2000), are rarely effective (except in isolated areas or before alien species have spread too widely; Simberloff 2003), and may have a greater negative impact on native communities than on the non-native species targeted (Smith *et al.* 2006). Even when eradication is successful, invasive species may have already caused long-term changes to community structure and ecosystem function (Zavaleta *et al.* 2001). Preventing unintentional introductions by recognizing potential invaders early is therefore likely to be the most effective management option (Kolar and Lodge 2001). Nonetheless, the specific characteristics of certain invasive species that facilitate their establishment and spread are often difficult to pinpoint (Kolar and Lodge 2001) and ecologists are urged to search for these traits in order to design preventative measures for use against invaders.

In attempts to identify the characteristics of invasive species, birds are among the most studied taxa (Kolar and Lodge 2001; Duncan *et al.* 2003). Recent findings suggest that ecological plasticity, behavioral flexibility (Sol *et al.* 2005), and, in particular, the introduction effort or propagule pressure (ie number of individuals released or the number of introduction attempts; Cassey *et al.* 2004), have been positively related to successful invasions. However, it is worth noting that these findings refer to deliberate introductions, a global but now rare practice. Current bird invasions into non-native regions tend to be accidental, mostly as a result of pet birds escaping (Martí and del Moral 2003), so the specific traits that may be advantageous for successfully invading new environments could vary. On a simple level, the most common captive species should be the most likely to invade, purely because a greater number of these individuals is likely to escape (ie because of greater propagule pressure). An observant field ornithologist might then wonder why the most abundant captive-bred pet species, such as budgerigars or canaries, have not been recorded as common invasive species. It is known from translocations of game or threatened species within their native ranges that captive-reared animals are less likely to establish in a new location than wild-caught animals (Griffith *et al.* 1989). Thus, one could hypothesize that captive-bred pet species may have lost the skills necessary for life in the wild and are less successful as invaders than are wild-caught species traded on the pet market (Figure 1).

In a nutshell:

- Pet birds escaping from cages are the main source of current avian invasions by exotic species
- An analysis of the invasiveness of ~200 pet species in Spain shows that wild-caught, but not captive-bred species are potential invaders, regardless of their availability on the market
- Banning the wild-bird trade would be an easy and effective way of controlling current invasions and preventing future ones, while captive breeding can satisfy the social demand for pets, without substantial risk

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Does the wild-bird trade promote exotic invasions?

Between 5 and 10 million birds are captured annually in the wild, mainly in developing countries, for export to the pet markets of the developed world (Gilardi 2006). Other avian species have been bred in captivity for centuries. Examining current avian invasions in Spain (Panel 1), we assessed the hypothesis that birds' origins

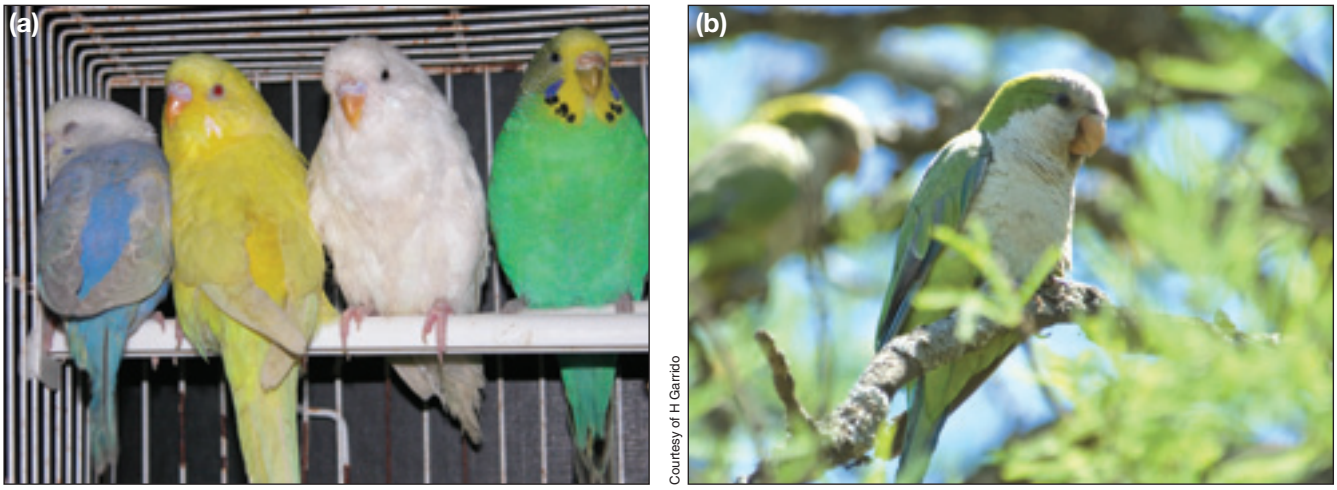

Figure 1. *Two parrot species with different degrees of invasiveness. (a) The captive-bred Australian budgerigar* (Melopsittacus undulatus) *is one of the most common pet species worldwide, but has never been recorded as an invasive species. Note the diversity of color mutations artificially selected in captivity. (b) On the other hand, the monk parakeet* (Myiopsitta monachus)*, a wild-caught species imported from Argentina, has formed feral populations in countries such as the US, Puerto Rico, Italy, Belgium, the Czech Republic, and Spain. Spanish populations are widespread and are increasing at an annual rate of ~20% (Martí and del Moral 2003), despite being 30 times more scarce as a caged bird than the budgerigar.*

(wild-caught versus captive-bred) could be a predictor of their invasiveness, regardless of their availability as pets. In Spain, the number of exotic bird species recorded (224) or breeding (50) in the wild is of great concern, particularly when compared to the number of native breeding species (288; Martí and del Moral 2003). Our results were straightforward: while captive-bred birds greatly outnumbered wild-caught birds as pets, the latter are more successful invaders (Figure 2 in Panel 1).

The ability to cope with new environments seems to have been lost in species bred in captivity over a long period of time. Captive-bred birds are often descended from a small pool of individuals, so the detrimental effects of inbreeding depression, loss of genetic diversity, and accumulation of deleterious mutations are to be expected (Charlesworth and Charlesworth 1987; Keller and Walter 2002). Endogamy (ie mating between relatives) is further promoted by breeders who artificially select the phenotypes that are now characteristic of many captive-bred species (Figure 1). Inbreeding depression can affect most fitness components, causing reduced viability, fecundity, and mating success, as well as slower development and increased susceptibility to pathogens and environmental stress (Charlesworth and Charlesworth 1987; Keller and Walter 2002). Perhaps more importantly, cultural knowledge, anti-predator, and foraging behaviors, which constitute important skills in the wild, can be eroded in captivity (McDougall *et al.* 2006). Artificial selection of certain phenotypes and/or genotypes in captivity can also promote sensory alterations (eg auditory and song abnormalities; Wright *et al.* 2004) that interfere with both natural and sexual selection. All of these problems make it difficult for captive-bred birds to survive after escaping and to establish breeding populations in the wild. Wild-caught birds, on the other hand, are collected by the millions in their natural habitats and, after severe post-capture mortality, we presume that only high-quality individuals remain alive to become pets. Humans may thus unintentionally induce artificial selection that favors wild-traded against captive-bred species as potential invaders. Moreover, some specific traits of birds that are associated with the success of deliberate introductions carried out in the past (Duncan *et al.* 2003; Cassey *et al.* 2004; Sol *et al.* 2005) might also play a role in current, accidental invasions. Nonetheless, the key issue is that the origin of birds used as pets may predict their ability as invaders, constituting a simple indicator of invasive potential, a metric difficult to assess in most biological invasions (Kolar and Lodge 2001; Puth and Post 2005). This means that, in terms of effective management, any proposal for banning the trade in wild birds could help to halt the spread of invasions already underway and to prevent future ones.

At this point, one could argue that all captive-bred species were originally wild-caught and, thus, that they could have been invaders in the past. In fact, ancient cultures from Europe, Asia, and America are known to have caught, kept, and bred birds as pets beginning as early as 4000 years before present. However, throughout most of history, bird keeping was primarily for the wealthy, and thus affected few birds and species. This activity did not become generally popular until just a few decades ago, encouraged by improved international transport capacity, which permits the commerce of millions of birds annually (BirdLife International 2000). Given the importance of pet availability (Panel 1) and propagule pressure in general for determining invasiveness, it seems likely that there were fewer opportunities for successful pet-bird invasions in the distant past.

Panel 1. The case of exotic bird invasions in Spain

Detailed information available on invasive birds in Spain (GAE–SEO/BirdLife 2006) allowed us to test the hypothesis that wild-caught pet species are better invaders than captive-bred ones. For this purpose, we categorized invasion success by exotic species using a scale that covers the gradient from accidental release to invasion (Kolar and Lodge 2001): 0 = available in the pet market, but never seen in the wild; 1 = seen occasionally in the wild; 2 = breeding irregularly in the wild; and 3 = breeding regularly, with self-sustaining or increasing wild populations. Data on pet abundance and pet origins (wild-caught versus captive-bred) was collected by counting the number of birds available from three major companies that supply birds on a national scale, every 2 weeks from September 2004 to October 2005 (ie until the first EU wild-trade ban). When more than one origin was recorded, the predominant one (ie the origin of more than 90% of individuals) was included in the analysis. The total number of individual birds counted throughout the study period was used as a measure of propagule pressure for each species. For species known to be free-living but not registered in market surveys, we estimated their availability as minimal (0).

Of the 21 315 birds recorded for sale on the Spanish pet market, passerines (songbirds) and parrots represented nearly 99% of all individuals recorded (61% and 38%, respectively) and so we only analyzed information for these two orders. The resulting dataset (see WebTable 1) comprised 202 species (130 passerines and 72 parrots). Seven species were not included in the analysis because of their obligate brood parasitism (which may impair their invasive ability) or doubts about their origin (see WebTable 1). Generalized linear mixed models (using the cumulative logit link function and the multinomial error distribution for categorical, ordered data; GLIMMIX procedure in SAS 9.1) were performed to investigate the relative influence of species' origin and their availability on the market, while controlling for potential phylogenetic effects (family and order as nested random factors; Sol *et al.* 2005).

Invasion success of pet species was positively associated with the number of individuals available on the market ($F_{1,176}$ = 6.92, P = 0.009), but was much more strongly associated with their origin (wild-caught versus captive-bred, $F_{1,176}$ = 33.27, P < 0.0001), while controlling for phylogenetic effects (Figure 2).

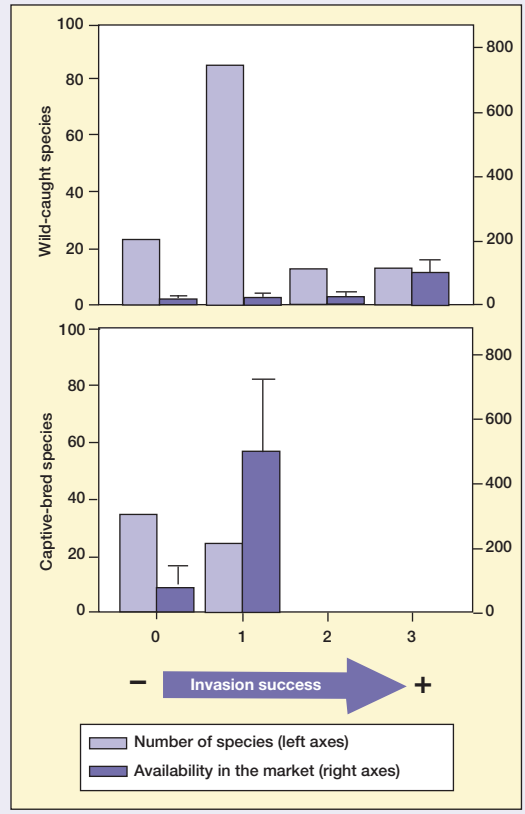

Figure 2. *Invasiveness of pet bird species in Spain in relation to their origin (wild-caught or captive-bred). Number of species and their availability (mean number of individuals ± SE) on the pet market are shown for each stage of the invasion process.*

Implications of banning trade in wild birds

The above view of current bird invasions adds evidence for trading as a source of biological invasions in a globalized world (Meyerson and Mooney 2007), and has important implications for the current battle regarding wild-bird trade bans (Senior 2006). After Australia halted trade in the 1950s and following US bans in 1992, most of the international wild-bird trade was redirected toward Europe. However, in October 2005, the European Union (EU) temporarily banned this trade, after imported birds died from the H5N1 strain of bird flu in the UK (Senior 2006). Subsequently, a coalition of 240 conservation and animal-welfare organizations began to campaign for a permanent halt to EU imports (World Parrot Trust 2004) on the basis of three concerns regarding trade in wild birds: (1) the spread of infectious diseases, (2) animal welfare, and (3) impacts on wildlife conservation in exporting countries. The wild-bird trade has been invoked as a major threat for many endangered species (BirdLife International 2000), although there is a scarcity of sound conservation science to assess its real impact (but see Wright *et al.* 2001). Remarkably, no serious monitoring program currently exists to examine the effects of trade on wild-bird populations or to look for ways to make it sustainable (Gilardi 2006). In fact, some conservationists defend the wild-bird trade as a way of sustaining native communities and associated wildlife, thereby avoiding illegal poaching and trade (Cooney and Jepson 2006) that could, in turn, increase the risk of spreading disease (ABC 2005). The European Commission (2007) has recently proposed a permanent ban on the wild-bird trade, citing risks to animal and human health and animal welfare. This resolution was approved by all EU member nations, despite the reluctance of some to accept economic losses or to contravene the Convention on International Trade in Endangered Species (CITES), which defends a strictly regulated wild-bird trade to help the conservation of sustainable populations of birds in exporting countries, as well as to avoid illegal trading (CITES 2007). The international illegal trade of parrots, however, does not seem to have increased after local protection of parrot species was instituted in different parts of the world (Wright *et al.* 2001; Pain *et al.* 2006), although it may remain substantial in some countries (Cantú *et al.* 2007). On the other hand, the acceptance of this ban without exceptions would benefit the biodiversity of importing countries by reducing

Figure 3. *The widespread availability of birds for sale in pet shops reflects an increasing social demand in today's largely urban society.*

their risk of biological invasion, a hitherto neglected conservation problem.

The EU has opted for a blanket ban (ie a ban irrespective of the conservation status of the species), in contrast to the US moratorium that only applies to endangered species listed by CITES (Wild Bird Conservation Act 1992). This moratorium does not eliminate all risk to the US because invasive potential would presumably be higher for non-endangered species, given that such species would be present on the market in greater numbers than endangered species (see the significant effect of pet availability on invasiveness in Panel 1). Moreover, the wild-bird trade produces considerable economic benefits in many countries throughout the world (Cooney and Jepson 2006) and international trade is expected to be redirected to other countries after the EU ban. Demand for pets is increasing, not only in developed countries, but also in developing countries such as Mexico, where imports of exotic parrots have increased eight-fold in the past decade and include ten wild-caught and potentially invasive species among those most imported (Cantú *et al.* 2007). Applying the precautionary principle (but bearing in mind the need for more studies to test the hypothesized link between invasive species and pets in other regions), a worldwide ban on wild-bird trading should be seriously considered.

Reconciling conservation threats and social demands

People need alternative solutions rather than prohibitions when conflicts between socioeconomic and conservation interests arise. A simple solution to the problem of invasion by exotic species sometimes extolled by conservationists is to eliminate the practice of keeping caged birds at home altogether. This would be a difficult, if not impossible task, since people have kept birds as pets for centuries, it is currently one of the most popular hobbies in the world, and social workers and other health-care professionals believe that pets help many people to lead healthier, happier lives (Figure 3). The development of captive breeding programs as the sole pathway for obtaining caged birds could solve this conflict by making the increasing demands on the pet-bird business, which moves ~200 million euros ($283 million) in countries such as Germany annually (www.pet-global.com), fully compatible with invasion prevention.

The captive-breeding solution, however, would seem to solve only conflicts affecting developed countries, and would not help those developing countries that currently export wild-caught birds. It has been argued that the banning of the wild-bird trade would impoverish communities, remove economic incentives for protecting bird habitat, and hamper conservation efforts in developing countries (Cooney and Jepson 2006; CITES 2007). Captive breeding could be an economic alternative for these source countries, as it has been in developed countries since the implementation of trade bans on some species (Roe 2006). Moreover, source countries have advantages, such as the availability of native birds for initiating captive-breeding stocks, favorable climates, and low production costs, all ideal conditions for competitive production of captive-bred pets for export to developed countries. Importing countries should make an effort to encourage bird breeders in developing countries and to register them as traders of captive-bred birds (CITES 2007), while ensuring that wild-caught birds are not laundered through the trade of captive-bred animals. If habitats are lost as a potential source of wild-caught birds, ecotourism programs might help to make their preservation economically attractive again. For example, it is well known that parrots have great appeal worldwide, a fact that has yet to be exploited by international sustainable ecotourism aimed at conserving threatened species and their habitats (Christian *et al.* 1996). A newer approach for protecting birds and associated habitat could be nest sponsorship through the payment of an annual sum, as in a program for parrot-nest sponsorship in Argentina (Parrot People 2007), which serves as an alternative to the harvest of parrot chicks for the pet trade (Gilardi 2006). These and other imaginative ideas are needed to involve all stakeholders and fully rec-

oncile the social, economic, and environmental needs of the pet trade in today's globalized world.

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WebTable 1. Complete data file used in the article, including species, degree of invasiveness, origin, and market availability

	Invasion success	*Market availability (# individuals)*	*Main origin*
Order Passeriformes			
Family Tyrannidae			
Tyrannus savana	1	0	wild
Family Pycnonotidae			
Pycnonotus bimaculatus	1	0	wild
Pycnonotus cafer	3	0	wild
Pycnonotus jocosus	1	0	wild
Pycnonotus leucogenys	1	0	wild
Pycnonotus xanthopygos	1	0	wild
Family Timaliidae			
Garrulax leucolophus	1	0	wild
Leiothrix lutea	3	8	wild
Family Corvidae			
Corvus albus	1	0	wild
Corvus ruficollis	1	0	wild
Corvus splendens	1	0	wild
Cyanocorax chrysops	1	0	wild
Urocissa erythrorhyncha	1	0	wild
Family Sturnidae			
Acridotheres cristatellus	1	0	wild
Acridotheres ginginianus	1	0	wild
Acridotheres tristis	2	0	wild
Aplonis metallica	1	0	wild
Cinnyricinclus leucogaster	0	2	wild
Gracula religiosa	1	5	wild
Gracupica (=Sturnus) nigricollis	2	0	wild
Lamprotornis (=Spreo) superbus	1	0	wild
Lamprotornis caudatus	2	0	wild
Lamprotornis chalybaeus	2	2	wild
Lamprotornis purpureus	1	0	wild
Sturnia (=Sturnus) malabaricus	1	0	wild
Sturnia (=Sturnus) sinensis	1	0	wild
Sturnus pagodarum	0	1	wild
Family Passeridae			
Passer (=Auripasser) luteus	1	18	wild
Family Ploceidae			
Euplectes afer	3	142	wild
Euplectes ardens	1	0	wild
Euplectes axillaris	1	0	wild
Euplectes franciscanus	1	165	wild
Euplectes hordeaceus	1	3	wild
Euplectes jacksoni	1	0	wild
Euplectes macrourus	1	33	wild
Euplectes nigroventris	1	0	wild
Euplectes orix	2	97	wild
Euplectes progne	1	0	wild
Ploceus (velatus) vitellinus	1	0	wild
Ploceus castaneiceps	1	0	wild
Ploceus cucullatus	2	11	wild
Ploceus galbula	2	0	wild
Ploceus intermedius	1	0	wild
Ploceus manyar	1	0	wild
Ploceus melanocephalus	3	0	wild
Ploceus nigerrimus castaneofuscus	1	0	wild
Quelea erythrops	1	0	wild
Quelea quelea	3	56	wild

(Continued)

WebTable 1. (*continued*)

	Invasion success	*Market availability (# individuals)*	*Main origin*
Family Estrildidae			
Aegintha temporalis	0	2	captive
Aidemosyne modesta	0	57	captive
Amadina fasciata	1	605	wild
Amandava amandava	3	2	wild
Amandava formosa	1	0	wild
Amandava subflava	1	18	wild
Chloebia (=Erythrura) gouldiae	1	772	captive
Clyptospiza monteiri	0	2	wild
Clyptospiza reichenovii	0	4	wild
Emblema guttata	0	26	captive
Emblema picta	0	8	captive
Erythrura cyaneovirens	0	1	captive
Erythrura prasina	1	0	wild
Erythrura psittacea	0	9	captive
Erythrura trichroa	0	1	captive
Estrilda astrild	3	286	wild
Estrilda caerulescens	1	74	wild
Estrilda erythronotos	0	4	captive
Estrilda melpoda	3	347	wild
Estrilda perreini	1	0	wild
Estrilda rhodopyga	1	0	wild
Estrilda troglodytes	3	323	wild
Euchistospiza dybowskii	0	21	wild
Lagonosticta rara	0	3	wild
Lagonosticta rubricata	0	4	wild
Lagonosticta senegala	1	34	wild
Lonchura (=Euodice) cantans	0	50	wild
Lonchura (=Euodice) malabarica	1	2	wild
Lonchura atricapilla	1	0	wild
Lonchura bicolor	1	1	wild
Lonchura castaenothorax	0	4	captive
Lonchura cucullata	0	37	wild
Lonchura fringilloides	0	28	wild
Lonchura griseicapilla	0	6	captive
Lonchura maja	1	0	wild
Lonchura malacca	2	0	wild
Lonchura punctulata	1	4	wild
Lonchura striata var domestica	1	501	captive
Mandingoa nitidula	0	20	wild
Neochmia ruficauda	0	80	captive
Nesocharis capistrata	0	1	wild
Ortygospiza atricollis	0	5	wild
Padda oryzivora	1	1349	captive
Poephila acuticauda	0	258	captive
Poephila bichenovii	1	83	captive
Poephila cincta	0	8	captive
Poephila (=Taeniopygia) guttata	0	2132	captive
Pyrenestes sanguineus	0	20	wild
Pytilia hypogrammica	0	23	wild
Pytilia melba	1	2	wild
Pytilia phoenicoptera	1	25	wild
Taeniopygia castanotis	1	0	captive
Uraeginthus bengalus	1	22	wild
Uraeginthus cyanocephala	0	4	wild

(Continued)

WebTable 1. (*continued*)

	Invasion success	*Market availability (# individuals)*	*Main origin*
Family Fringillidae			
Carduelis cucullata	0	6	captive
Carduelis magellanica	0	1	captive
Carduelis yarrellii	1	0	wild
Eophona migratoria	1	0	wild
Pyrrhula erythaca	1	0	wild
Rhodopechys (=Rhodospiza) obsoleta	1	4	wild
Serinus atrogularis	1	0	wild
Serinus canaria	1	4501	captive
Serinus dorsostriatus	1	0	wild
Serinus flaviventris	0	1	wild
Serinus leucopygius	0	129	wild
Serinus mozambicus	1	298	wild
Serinus pusillus	1	0	wild
Sporopipes squamifrons	0	2	wild
Family Cardinalidae			
Cardinalis cardinalis	1	0	wild
Family Emberizidae			
Emberiza caesia	1	0	wild
Paroaria capitata	1	0	wild
Paroaria coronata	2	0	wild
Paroaria dominicana	1	0	wild
Sicalis flaveola	1	22	wild
Family Icteridae			
Dolichonyx oryzivorus	1	0	wild
Sturnella loyca	1	0	wild
Sturnella magna	1	0	wild
Family Thraupidae			
Euphonia clorótica	0	4	captive
Family Viduidae			
Vidua chalybeata[1]	1	10	wild
Vidua fischeri[1]	1	0	wild
Vidua macroura[1]	1	188	wild
Vidua paradisea[1]	1	14	wild
Order Psittaciformes			
Family Psittacidae			
Agapornis canus	1	4	wild
Agapornis fischeri[2]	2	578	captive
Agapornis lilianae	1	0	captive
Agapornis nigrigenis	0	21	captive
Agapornis personatus[2]	2	531	captive
Agapornis pullarius	1	0	captive
Agapornis roseicollis	1	1062	captive
Amazona aestiva	2	26	wild
Amazona amazonica	1	61	wild
Amazona farinosa	1	4	wild
Amazona festiva	1	0	wild
Amazona ochrocephala	0	25	captive
Ara ararauna	1	16	wild
Ara chloroptera	0	1	wild
Ara macao	1	0	wild
Ara (=Orthopsittaca) manilata	0	7	wild
Ara (=Diopsittaca) nobilis	1	0	wild
Ara rubrogenys	1	0	captive
Ara severa	1	0	wild
Aratinga acuticaudata	3	64	wild
Aratinga aurea	1	1	captive
Aratinga erythrogenys	3	6	wild
Aratinga holochlora	1	0	wild
Aratinga jendaya	0	5	captive

(Continued)

WebTable 1. (*continued*)

	Invasion success	*Market availability (# individuals)*	*Main origin*
Aratinga leucophthalmus	1	0	wild
Aratinga mitrata	3	58	wild
Aratinga pertinax	1	26	wild
Aratinga solstitialis	0	4	captive
Barnadius zonarius	0	1	captive
Bolborhynchus lineola	0	33	captive
Brotogeris tirica	1	0	wild
Cyanoliseus patagonus	2	143	wild
Cyanoramphus auriceps	0	2	captive
Cyanoramphus novaezelandiae	0	111	captive
Eclectus roratus	1	2	captive
Eos bornea	1	1	wild
Forpus coelestis	0	41	captive
Forpus passerinus	1	2	captive
Lathamus discolor	1	0	captive
Lorius garrulus	1	0	wild
Melopsittacus undulatus	1	2878	captive
Myiopsitta monachus	3	95	wild
Nandayus nenday	2	16	wild
Neophema (=Neopsephotus) bourkii	0	31	captive
Neophema elegans	0	17	captive
Neophema pulchella	0	38	captive
Neophema splendida	0	11	captive
Pionus maximiliani	1	20	wild
Pionus menstruus	0	12	wild
Pionus senilis	0	3	wild
Platycercus adscitus	0	8	captive
Platycercus elegans	1	57	captive
Platycercus eximius	1	237	captive
Platycercus flaveolus	0	5	captive
Platycercus icterotis	1	10	captive
Poicephalus crasus	1	0	wild
Poicephalus senegalus	2	80	wild
Polytelis anthopeplus	0	8	captive
Polytelis swainsonii	0	6	captive
Psephotus haematonotus	1	128	captive
Psephotus varius	0	8	captive
Psittacula alexandri	1	0	wild
Psittacula eupatria	1	0	wild
Psittacula krameri[2]	3	65	captive/wild
Psittacus erithacus	1	305	wild
Pyrrhura frontalis	1	0	captive
Pyrrhura picta	0	12	wild
Trichoglossus haematodus	1	1	captive
Family Cacatuidae			
Cacatua galerita	1	1	captive
Cacatua ophtalmica	1	0	captive
Cacatua sulphurea	1	0	captive
Nymphicus hollandicus	1	1211	captive

Notes: [1]Species not included in analysis because of their parasitic reproductive behavior; [2]Species not included in analysis because of doubts about their origin (ie during our survey, most individuals were recorded as captive-bred, but these species were mainly wild-caught in the recent past). When including the three species of doubtful origin, however, results were nearly identical (a stronger effect of the origin of species [$F_{1,179}$ = 28.67, P < 0.0001] than on market availability [$F_{1,179}$ = 7.32, P = 0.0075]).