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Escaping captivity: The biological invasion risk from vertebrate species in zoos

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ABSTRACT

Worldwide, invasive alien species increasingly contribute to environmental change and are a massive drain on social and economic resources. In Australia, the detection of new vertebrate incursions (i.e., alien species not currently established) has increased over the last decade. In other parts of the world, zoos have been identified as one of the influential pathways for the establishment of alien vertebrate species. We quantified the number of vertebrate species released (escaped and stolen) from Australian zoos between 1870 and 2010. The majority of reported releases (185 out of 230) have occurred since 1985. Most of the species (77.9%), which have escaped, or been stolen, from Australian zoos have only ever been released once. In sum, escapes were much more common (89%) than thefts. Compared to the other three vertebrate classes (amphibians, birds, mammals) reptiles experienced a significantly greater proportion of thefts than expected by chance. Almost half of all escapes (46%) were bird species. Birds also had the lowest retrieval rate, and therefore posed the greatest potential risk to establishment and subsequent invasion. We used phylogenetic logistic regression models to assess the association of evolutionary traits correlated with the propensity of a bird species for escaping. There was only weak evidence of phylogenetic signal (association among related species) in the tendency of a bird to escape. Bird species were significantly more likely to have escaped if their current total collection size was larger. There was no relationship between escape and the type of holding (aviary versus free-range/open-pond), or life history traits (adult body size and geographic breeding range size). Zoos are a prominent part of our culture and play a valuable role in education and conservation. Captive animals, including those in zoos, are subject to release, through both intentional and unintentional pathways, however, the establishment of alien species associated with Australian zoos is extremely low. We conclude that, in Australia, the risk of introduction by alien species from zoos is low, and substantially less than other 'backyard' and illegal sources of private species keeping and trade.

1. Introduction

Invasive alien species are a key driver of human induced environmental change and global species extinctions (Vitousek et al., 1997; McGeoch et al., 2010; Simberloff et al., 2013), and a massive drain on international economic resources (Pimentel et al., 2001; Hulme, 2009; Marbuah et al., 2014). In Australia, a recent conservative estimate of the annual direct economic impact of widespread terrestrial alien vertebrate pests (excluding their considerable environmental and social costs) was AU$743 million, with annual research and management costs exceeding AU$122 million (Gong et al., 2009). In addition, the detection of new vertebrate incursions (i.e., alien species not currently established in Australia) has increased over the last decade (Henderson et al., 2011). Whereas, the majority of new alien vertebrate species detections (c. two-thirds) were intercepted by border security agencies (illegally smuggled or unintentionally stowed-away), a substantial number (76 species of 186 in total) had escaped (or were stolen) from post-border collections, or confiscated from the illegal pet trade (Henderson et al., 2011).

The potential for any animal to be released from captivity poses a number of post-border biosecurity risks (Hulme et al., 2008), and releases of alien species can pose severe economic, environmental and social threats (Pyšek and Richardson, 2010). The term release covers a variety of circumstances, which differ in their degree of human intention. These circumstances can range from unforeseen events, such as an environmental accident that compromises the integrity of a confinement barrier, to an owner who, in times of hardship (e.g., financial or psychological), opens the collection

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gates. However, in most circumstances releases of zoo animals, in particular, are either unintentional escapes or intentional thefts.

The keeping of wild animals dates back to their earliest domestication, which became commonly practiced around 12 k years ago (Vigne, 2011). However, the exhibition of captive animals did not arise until after the urbanization of civilization around 5 k years ago (Kisling, 2001). Queen Hatshepsut of Egypt is recorded to have constructed a zoological garden for the ceremonial display of large-bodied wild animals around 3.5 k years ago (Livingston, 1974). Similar exhibitions were established by rulers in China, India and Africa as a display of their wealth and power (Kisling, 2001). In the ancient Mediterranean region, there was keen interest in alien species for exhibition in menageries and gardens, and for their slaughter in the arenas. An international trade developed in particular species that could be maintained in captivity (Jennison, 1937). From the 15th century, European explorers discovered an enormous range of new species during their global explorations, and established zoos in Britain and continental Europe on their return. The popular modern zoological collection, for public viewing, arose in the early part of the 19th century with the cities of London, Paris and Dublin opening zoos within a few years of each other (Strehlow, 2001). By 2011, 837 zoos worldwide, which were International Species Information System (ISIS) members, contained 3955 alien terrestrial vertebrate species; 58% were birds, 25% were mammals, 11% were reptiles and 6% were amphibians (Conde et al., 2013).

In Europe, zoos have been identified as the second most important known pathway (following the pet trade) for the introduction of escaped alien vertebrate species (Hulme et al., 2008). However, these introductions are dwarfed by the number of species intentionally released for food/game and fauna improvement. It was also found that European zoos, which did not belong to a professional association, had more non-secure enclosures than zoo association members (Fàbregas et al., 2010). In Australia, alien vertebrate species, particularly mammals, reptiles and amphibians, are not as readily legally available as pets, in comparison to much of Europe and the USA, or non-Western countries. Although no widespread alien vertebrate pest species has ever originated from an Australian zoo, at least, two free-living populations have established via species released from captive collections. In Perth, a wild population of the five-lined palm squirrel (*Funambulus pennanti*), native to south Asia, was descended from captive animals intentionally released into the zoo grounds by the local Acclimatisation Society in 1898 (Long, 2003). In Tasmania, a localised population of the agile wallaby (*Macropus agilis*) originated from a small number of individuals that escaped (or were intentionally released) from a wildlife park in the late 1990s (Pauza et al., 2014). Native to mainland Australia, the introduced population on Tasmania occurs outside its natural geographic range.

Scientific accounts of zoo releases are relatively rare (Fàbregas et al., 2010). Nevertheless, in Australia, as well as the rest of the world, there are numerous records (and anecdotal accounts) of animal releases from zoos (Csurshes, 2003). Examples of these accounts include:

[1] The Northern Territory (Australia) pig-hunter who 'accidentally' shot a pygmy hippo (*Choeropsis liberiensis*) in the Douglas Daly district 200 km south of Darwin, in November-2009. Native to western African it was believed that the female pygmy hippo had *escaped* from a former private collection on Tipperary Station, which was closed in 2003; 6 years prior to the shooting (http://www.abc.net.au/news/2009-11-16/nt-man-shoots-pygmy-hippo-by-mistake/1145336).

[2] The 25 kg alligator snapping turtle (*Macrochelys temminckii*) discovered in a stormwater drain in a Sydney suburb (Australia) in 2000, after a heavy rain event. Native to waterways in the south-eastern United States, the alligator snapping turtle is the largest freshwater turtle (by weight) in the world, and it required six council workers and a wheelbarrow to remove the male turtle from the stormwater drain. It was believed that the turtle could have been one of a batch of juveniles *stolen* from an Australian fauna park near Sydney in 1979; 21 years prior to its recovery (http://www.theguardian.com/world/2000/nov/29/patrickbarkham).

[3] The *intentional release* of dozens of wild alien carnivores and primates in October-2011 from a preserve in Ohio (United States), following the suicide of the preserve's owner. The majority of the wild animals, which included over 30 Bengal tigers (*Panthera tigris tigris*) and lions (*Panthera leo*), were fatally controlled, however, a single macaque (*Macaca* sp.) was never recovered (http://abcnews.go.com/US/zanesville-animal-massacre-included-18-rare-bengal-tigers/story?id=14767017).

Collectively, these accounts lead to the inference that large species collections can be a prominent pathway for the post-border release of alien (and potentially invasive pest) species (see also Hulme et al., 2008). In the current paper we analyse the historical release of animals (alien and native) from 19 Australian zoos (1870–2010) and provide a quantitative appraisal of the biological invasion risk from vertebrate species in zoo collections. Specifically, we tested for differences among vertebrate classes (amphibians, birds, mammals, reptiles) in their propensity for escaping (and being stolen) from zoo collections, as well as their likelihood of (and time to) retrieval. We also compared characteristics of the different zoo collections, and whether the frequencies of releases have changed through time. For the one vertebrate class which has experienced the majority of zoo escapes (Aves) we quantitatively tested whether a set of putative species-level and collection-level characteristics were associated with a species' propensity for escaping.

2. Data and methods

2.1. Zoo release data

The list of vertebrate species in Australian zoological collections follows the Zoo and Aquarium Association (ZAA) '*Australasian Species Management Program: Regional Census and Plan*' (Hibbard and Wilkins, 2010). The list of alien species in Australia follows the Australian intergovernmental Vertebrate Pest Committee (VPC, 2007) and sources therein. In Australia, the display (and import) of alien wildlife is legislated for under the *Quarantine Act* 1908 and the *Environment Protection and Biodiversity Conservation Act* 1999 (EPBC Act), with the regulatory authorities of each of the States and Territories controlling the movement (import and export) of alien wildlife within the country. Under the EPBC Act, the Australian Government established the *List of Specimens taken to be Suitable for Live Import* (last updated 26-May-2014: http://www.environment.gov.au/biodiversity/wildlife-trade/live/import-list), which regulates the particular species that can be imported into the country through the assessment of potential risks of an alien species to Australia (Bomford, 2008).

Australian State and Territory legislative bodies were contacted (by email and telephone) to determine the number of all exhibited animal licence holders, and the number of those holding alien species. This information was used to determine what proportion of exhibited licence holders, who held alien species, were members of the ZAA. The ZAA is the peak body representing the zoo and aquarium community throughout Australasia, and is a member of the World Association of Zoos and Aquariums. In 2012, there were 38 alien species licences in Australia of which 30 institutions

(c. 80%) were members of the ZAA. In order to qualify for membership to the ZAA, institutions need to demonstrate industry best practice in the welfare and display of animals, financial viability, and succession planning. Upon application to the ZAA institutions are required to provide a copy of their policies for industry peer-review including; in the event of closure, animal escape policy and procedure, working with potentially dangerous animals, security strategy, pest management, and acquisition and disposition of animals. In 2012, information regarding the releases (escapes and thefts) of zoo species was requested from all Australian members of the Zoo and Aquarium Association.

Data collected from the institutions included: (i) year the institution was established; (ii) location of the institution, i.e., Australian State or Territory; (iii) total number of vertebrate animal species; and (iv) total number of specimens held. In addition, institutions were asked to provide the following information relating to the number and identity of any reported releases: (v) type of release (escape or theft); (vi) date of release (year and month); (vii) species identity (common and scientific name); (viii) number of individuals released; (ix) fate of the individuals (i.e., whether they were successfully retrieved or not); (x) the amount of time (in days) to retrieval, if successful; and (xi) a full description of zoo security, including whether or not 24-h manned security was present. Escapes from enclosures were only included if the individual had managed to escape beyond the perimeter fence, or no perimeter fence was present.

Due to the nature of record keeping, definitive electronic records were only available for 17 zoos from 1985 to 2010. Historical records were collected from 1930 to 1987, using zoo archival records. In addition, searches of old newspaper archives were conducted to establish any escapes or thefts from zoos from 1870 through to 1987. Requests were made to the respective institutions for any further information regarding newspaper archive data. Finally, State and Territory legislative authorities were approached for their release data, which is collated from animal record sheets submitted to the authorities by the zoos.

The greatest numbers of escapees (total species and number of individuals) were bird species (c. 46% of all escape events; see Section 3). In addition, to having the highest rate of escape, birds had the lowest retrieval rate (see Section 3), and therefore pose the greatest potential risk to establishment and subsequent invasion. Species-level bird data was collated from the four largest public zoo collections in Australia, which had accurate electronic records of all bird escapes between 1990 and 2010. These four institutions provided the following information: the number of bird species held, and number of individual bird specimens held in each year; including the number of alien bird species and specimens held (ZAA Census plan 1990–2010). Species were scored, from ZAA records, as to whether they are regularly maintained in enclosed aviaries or open-yards and walk-through ponds. We compiled life-history traits for birds (adult body mass and breeding geographic range) using a comprehensive survey of the ornithological literature (Dunning, 2008; del Hoyo et al., 1992–2002, 2003–2011) and previously published datasets (Orme et al., 2005, 2006; Olson et al., 2009). Body size in birds is one of the most fundamental life history parameters and subsumes much of the variation in avian reproduction and demography (Bennett and Owensm, 2002). Body mass was estimated as the adult geometric average (g). Alternately, geographic range sizes in birds are much less constrained by phylogenetic relatedness, and more likely to reflect interactions between a species ecological and habitat preferences and current dispersal opportunities (Webb and Gaston, 2003). Breeding geographic range (km^2) was based on a previously reported database (Orme et al., 2005) of distribution maps for land bird species, which were mapped as vectors or "polygons" and converted to an equal area grid for analysis (Orme et al., 2006).

2.2. Analytical methods

All analyses were conducted in the statistical software program R version 3.0.2 (R Core Team, 2013). Contingency-type frequency tests for assessing, and visualising, the independence of categorical variables were conducted in the graphical package 'vcd' for visualising categorical data (Friendly, 2000; Zeileis et al., 2007; Meyer et al., 2013). The homogeneity of frequencies was evaluated with Wald Chi-square tests for independence. We tested the homogeneity of survival curves for the length of time (number of days to retrieval) across classes (amphibians, birds, mammals, reptiles) in the package 'survival' (Therneau and Grambsch, 2000; Therneau, 2014). We conducted bespoke randomisation tests to assess the likelihood of a randomly chosen species, from the same zoo as an escaped species, having a higher rank abundance in the collection than the escaped species. We compared the observed median rank abundance, across all zoo collections, to the distribution of expected ranks averaged across 10,000 simulations. A smaller proportional rank means that the species have a larger median abundance, across the collections, than expected by chance. Generalised linear models were conducted to test the number of releases (escapes and thefts) through time (Poisson distributed errors and log link function), and for comparing the characteristics of different zoos (age of the collection, presence of security, collection size) in relation to the number of escapes and thefts. Model sets were assessed using Akaike Information Criterion corrected for small sample sizes (AICc), and relative model weights (Burnham and Anderson, 2002).

We tested the strength of the phylogenetic signal in the propensity of related bird species to escape captivity by coding whether or not a zoo species (both alien and native) has ever escaped (binary variable; not escaped = 0, escaped = 1) and calculating the binary phylogenetic signal strength D (Fritz and Purvis, 2010). Clearly, propensity for escaping is not an evolved trait, but it may be correlated with species traits that are, and the threshold model for calculating character dispersion on a phylogeny provides a way to scale phylogenetic signal strength under a specified evolutionary hypothesis (Fritz and Purvis, 2010). We tested whether there was evidence for observed D differing from 0 (expected phylogenetic structure resulting from a Brownian process of evolution) and 1 (expectation from zero or random phylogenetic structure) using the R package 'caper' (Orme et al., 2013). Avian phylogenetic trees were constructed online (birdtree.org) based on data from the complete avian phylogeny of Jetz et al. (2012) and using the primary backbone tree of Hackett et al. (2008). One hundred trees were constructed, and phylogenetic logistic regression (PLR) models (Ives and Garland, 2010) were conducted to test the association between whether or not a bird species has escaped and the total size of the zoo collections (sum of individuals in all collections [median = 39 individuals]), and the species life-history (adult body mass, breeding geographic range size).

PLR models were conducted in the R package 'phylolm' (Ho and Ane, 2014). The PLR model specifies the structure of the variance–covariance matrix reflecting the phylogenetic associations among the species, and also includes an estimated parameter that governs the strength of phylogenetic signal in the dependent variable. Thus, the PLR does not require the *a priori* assignment of phylogenetic signal but instead allows the data to dictate its magnitude in the statistical model (Ives and Garland, 2010). Phylogenetic models were assessed using Akaike Information Criterion (AIC), and relative model weights.

3. Results

3.1. Zoo release events

We report on 230 release events (independent escapes and thefts) of vertebrate species (both alien and native), from 19 Australian zoos, between 1870 and 2010. In the last three decades there has been a dramatic increase in the reported number of escapes from Australian zoos (Fig. 1). Most reported escapes (85.9%) have occurred since 1985. The number of reported thefts is also greatest for this period, with 44% of all reported zoo thefts occurring in the last decade (2001–2010) (Fig. 1). For the most recent period of definitive (electronic) reporting (1985–2010; $n = 26$ years), there has been an increase in both the number of reported escapes (slope ± std err = 0.271 ± 0.070, $t = 3.86$, $P < 0.001$) and the number of reported thefts (slope ± std err = 0.126 ± 0.035, $t = 3.59$, $P < 0.002$).

During the recent period of definitive electronic record-keeping (1985–2010), the total number of zoos in our dataset has increased from 11 in 1985 to 17 in 2010. There has been no significant change in the total number of specimens held (slope ± std err = 3.31 ± 7.80, $t = 0.42$, $P = 0.678$), however, the total number of vertebrate species held in these Australian zoos has actually decreased (slope ± std err = −2.49 ± 0.57, $t = -4.32$, $P < 0.001$). In a time-dependent model, which already included the variable year, the increase in the reported number of releases is not significantly associated with the increase in the number of zoos for either escapes (slope ± std err = 0.386 ± 0.476, $t = 0.81$, $P = 0.426$), or thefts (slope ± std err = 0.222 ± 0.238, $t = 0.94$, $P = 0.359$).

3.2. Characteristics of zoos from which animal releases have occurred: escapes versus thefts

The vast majority of reported animal releases from Australian zoos (both escapes and thefts) have occurred in the recent period of definitive electronic-reporting (84.8%). During this period 11 (out of 17) zoos reported animal releases. The number of vertebrate species, held by these zoos, was significantly greater for historical zoos (opened pre-1950, $n = 6$) than for the zoos opened more recently (difference in number of species ± std err = 0.884 ± 0.050, $z = 17.75$, $P < 0.001$). Ten of the 17 zoos had 24-h security (i.e., closed-circuit cameras, on-site guards, or a permanent caretaker). The presence of 24-h security was not related to the number of vertebrate species at the zoo (number of species ± std err = 0.001 ± 0.006, $z = 0.14$, $P = 0.892$), the total size of the zoo collection (Log_{10} number of individuals ± std err = −0.376 ± 0.721, $z = -0.52$, $P = 0.602$), nor the date the collection was opened (year ± std err = 0.004 ± 0.010, $z = 0.45$, $P = 0.650$).

In a Poisson generalised linear model the number of escapes (from a zoo since 1985) was best related to the age of the institution, the total size of the collection, and the absence of 24-h security, but was not significantly related to the number of vertebrate species in the zoo (Table 1). The number of thefts was best related to the age of the institution and the total size of the collection, but was not significantly related to the presence of 24-h security, nor the number of vertebrate species in the collection (Table 1).

3.3. Occurrence and retrieval of animal releases from zoos: escapes versus thefts

The vast majority (77.9%) of species that have escaped or been stolen from Australian zoos have only ever been released once. Of the species (both alien and native) that have been released on multiple occasions, the most frequent is the native koala (*Phascolarctos cinereus*), which has escaped at least nine times (from four different institutions); most recently in the last year of data reporting (Table 2).

On average, escapes were much more common (89%) than thefts (Fig. 2). Compared to the other three vertebrate classes (amphibians, birds, mammals) reptiles experienced a significantly greater proportion of thefts than expected by chance (Fig. 2; [Wald Chi-square = 9.39, df = 3, $P = 0.024$]). Across all four taxonomic classes, native reptiles were significantly more likely to be stolen (than alien reptiles) whereas native birds and mammals were significantly less likely to be stolen (Wald Chi-square = 34.31, df = 7, $P < 0.001$). There was no significant difference in the proportions of native and alien species that escaped for any of the four classes (Wald Chi-square = 6.37, df = 3, $P = 0.095$). The percentage of alien species escapes (compared with native species escapes), across all four taxonomic classes, was 50.5%.

No reported amphibian releases (eight escapes and two thefts) have ever been retrieved. The probability of successfully retrieving a released species differed significantly across the other three taxonomic classes (Fig. 3). Compared with mammals and reptiles, bird escapes were significantly less likely to be retrieved, and more likely to not be retrieved (Fig. 4). Conversely, compared with birds and reptiles, mammal escapes were significantly more likely to be retrieved, and less likely not to be retrieved (Fig. 4). Reptile thefts were significantly less likely to be retrieved than bird or mammal thefts (Fig. 4). There was no significant effect of release-type on the probability of being retrieved (escape versus theft; Wald

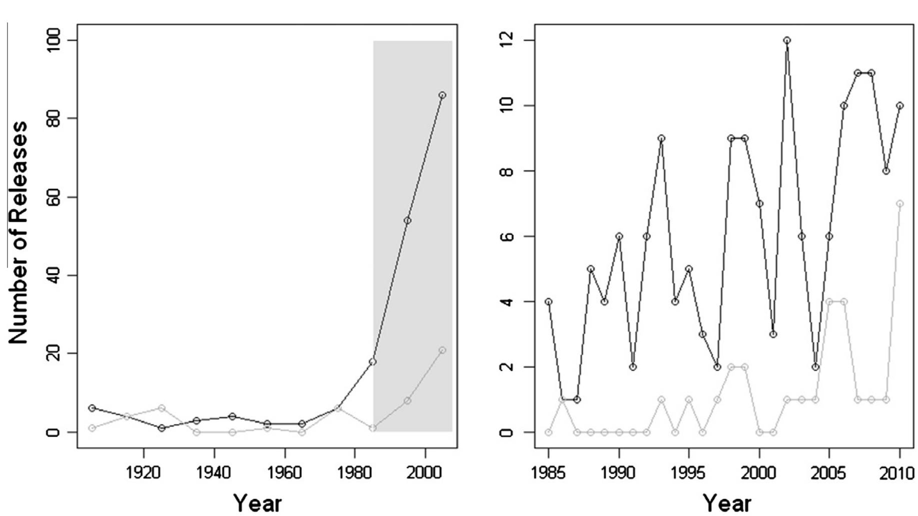

Fig. 1. The increase in frequency (count) of vertebrate releases (black line = escapes; grey line = thefts) from Australian zoos during the period: (a) 1870–2010 ($n = 19$ zoos) and (b) 1985–2010 ($n = 17$ zoos).

Table 1
Model support (AICc; Akaike's Information Criterion corrected for small sample sizes) for the top-ranked Poisson regression models of the number of release events (escapes and thefts) across 17 zoos between 1985 and 2010. Independent variables (estimates [std err]) in the models included: (i) the age of the zoo (historical, pre-1950; modern, post-1950); (ii) the presence (or absence) of 24-h security measures; (iii) the total number of vertebrate species in the zoo; and (iv) the total number of individuals, summed across all vertebrate species. Relative model weights were calculated across the entire model set and sum to one.

Intercept	Zoo age: modern (post-1950)	Security: 24-h	Log_{10} number of species	Log_{10} total number of individuals	AICc	ΔAICc	AIC model weights
Escapes							
−1.966 [0.937]	−1.530 [0.325]	−0.587 [0.181]		1.721 [0.295]	120.9	0.00	0.657
−1.669 [0.916]	−1.509 [0.332]	−0.530 [0.180]	−1.682 [1.047]	2.790 [0.736]	122.4	1.57	0.300
−0.880 [0.711]	−1.782 [0.310]		−2.074 [0.984]	2.744 [0.705	127.4	6.47	0.026
−1.012 [0.718]	−1.827 [0.217]			1.342 [0.217]	128.3	7.47	0.016
Thefts							
−4.508 [2.187]	−1.531 [0.765]			1.906 [0.652]	41.3	0.00	0.360
−8.435 [1.793]				3.040 [0.545]	42.4	1.16	0.202
−3.576 [1.892]	−1.945 [0.671]		2.332 [0.815]		44.0	2.71	0.093
−9.028 [2.038]		−0.427 [0.404]		3.302 [0.647]	44.3	3.03	0.079

Table 2
Species released (escapes and thefts) multiple times during the period of electronic reporting (1985–2010).

Scientific name	Common name	Release type	Frequency of releases	Last release date
Phascolarctos cinereus	Koala	Escape	9	2010
Psittacula krameri	Indian ringneck parrot	Escape	6	2002
Tadorna radjah	Raja shelduck	Escape	6	2007
Antaresia perthensis	Pygmy python	Escape	4	2009
Arctictis binturong	Binturong	Escape	4	2008
Litoria adelaidensis	Slender tree frog	Escape	4	2007
Ailurus fulgens	Red panda	Escape	3	2010
Alopochen aegyptiacus	Egyptian goose	Escape	3	2007
Aythya novaeseelandia	New Zealand Scaup	Escape	3	2004
Eclectus roratus	Eclectus parrot	Escape	3	2006
Ctenotus lancelini	Lancelin Island skink	Escape	2	2003
Cynops pyrrhogaster	Japanese red-bellied newt	Escape	2	2009
Gallicolumba luzonica	Bleeding-heart pigeon	Escape	2	2009
Grallina cyanoleuca	Magpie lark	Escape	2	2000
Hirundo neoxena	Welcome swallow	Escape	2	2002
Numida meleagris	Helmeted guineafowl	Escape	2	2008
Padda oryzivora	Javan sparrow	Escape	2	2010
Petrogale xanthopus	Yellow-footed rock wallaby	Escape	2	2005
Tachyglossus aculeatus	Short-beaked echidna	Escape	2	2009
Tiliqua scincoides	Common blue tongue	Escape	2	2005
Morelia spilota	Carpet python	Theft	4	2005
Morelia viridis	Green python	Theft	2	2006
Pogona vitticeps	Bearded dragon	Theft	2	2010

Chi-square = 2.60, df = 1, $P = 0.107$), or an interaction between taxonomic class and release-type (Wald Chi-square = 0.77, df = 2, $P = 0.680$). For those individuals that were retrieved, the retrieval time (i.e., how long (in days) the released individuals were at large) was significantly greatest for birds (mean number of days ± std err = 91.7 ± 59.9, $n = 7$) and least for mammals (2.8 ± 1.3, $n = 11$) (log-rank Chi-square [birds versus mammals] = 3.86, df = 1, $P = 0.049$).

3.4. Bird species escapes

Over a third of all vertebrate release events (escapes and thefts) were for bird escapes (Fig. 2). For birds that escaped between 1990 and 2010 (from the four largest zoos in Australia with electronic record keeping; $n = 32$ separate escape events), the observed median proportional rank abundance for the zoo collection of the escapee species (0.31) was significantly less (randomisation *P*-value < 0.001) than expected from a random choice of any species ($n = 32$ events) within the same collections (Supplementary Fig. S1). A smaller proportional rank means that the species had a larger median abundance, across the collections, than expected by chance.

For the bird species ($n = 22$) that have escaped from these four collections (1990–2010) compared with all the bird species in those collections ($n = 129$) there was no evidence of phylogenetic signal resulting from Brownian phylogenetic structure in the tendency of a species to escape (estimated median *D* [1st, 99th percentiles] = 0.794 [0.678, 0.897]; $k = 100$ phylogenetic models; all $P < 0.001$). Species were more likely to have escaped if their average total collection size was larger (Fig. 5a). Across 100 PLR models the median abundance for escapee species (c.f. with non-escaping species) was positive (estimate for Log_{10} abundance·year^{-1} [1st, 99th percentiles] = 2.06 [2.01, 2.22]) and highly significant (all $P < 0.001$).

In addition, for any bird species ever escaped ($n = 46$ species) compared with the Australian holdings for all bird species ($n = 279$) there was no evidence of phylogenetic signal resulting from Brownian phylogenetic structure in the tendency of a species to escape (estimated median *D* [1st, 99th percentiles] = 1.063 [0.996, 1.121]; $k = 100$ phylogenetic models; all $P < 0.001$). Species were significantly more likely to have escaped if their current total collection size (Log_{10} summed abundance) was larger (Fig. 5b). In a model set, which included: (i) total current collection size; (ii) type of holding (aviary versus free-range/open-pond); (iii) adult body size; and (iv) geographic breeding range size, the model with just total collection size was the top ranked model across 87 of the 100 phylogenies (Table 3). Total collection size was retained in all of the top eight models (median ΔAIC < 4.00), with a median variable importance (summed median relative model weight) of 0.97 (Table 3).

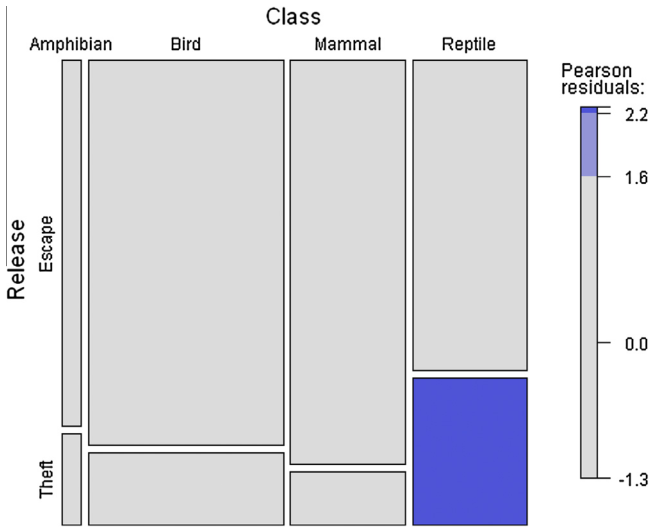

Fig. 2. Mosaic plot of the deviation in conditional independence between release type (theft, escape) and taxonomic class (amphibian, bird, mammal, reptile) for 230 release events from 19 Australian zoos between 1870 and 2010. The plot is constructed so that the size of each cell (rectangle) is proportional to the observed cell frequency for each trait. The residual-based shading follows Zeileis et al. (2007), and reflects the cell contribution to the Chi-square statistic: shades of blue, when the observed frequency is substantially greater than the expected frequency under independence, as shown in the legend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

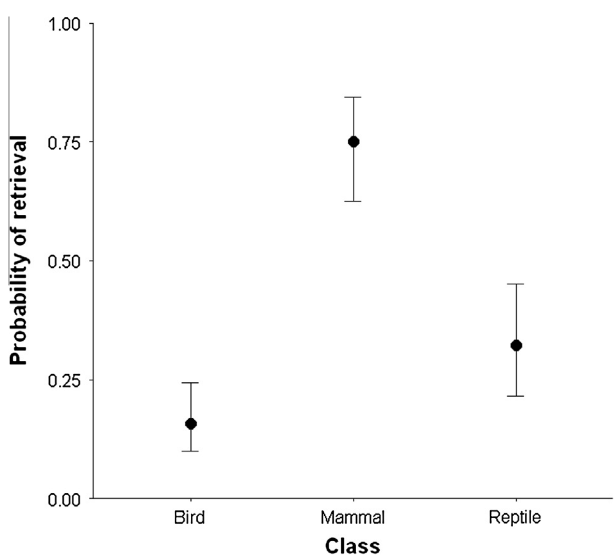

Fig. 3. The average probability (95% CI) of successfully retrieving a released species differed significantly across the three taxonomic classes pictured (Wald Chi-square = 46.99, df = 2, $P < 0.001$). No reported amphibian releases (eight escapes and two thefts) have ever been retrieved.

4. Discussion

Globally, approximately 26 billion animals, spanning over 10,000 species (alien and native), are kept on farms and in zoos, conservation breeding centres, research laboratories and private collections (Mason, 2010). It is clear that captive animals, including those in zoos, are subject to release, through both intentional and unintentional pathways. In Australia, escapes of vertebrate species from zoos have occurred much more frequently than thefts. Escape attempts may be motivated by a variety of behaviours (Mason and Rushen, 2008); for example, foraging, mate searching, or escaping from some aversive event (including confinement itself). Indeed, stereotypies (abnormal behaviour) in captive wild animals may arise from repeatedly thwarted (i.e., unsuccessful) attempts to escape confinement (Dantzer, 1986; Mason, 1991; Clubb and Vickery, 2006).

The zoo community is highly heterogeneous (Zimmermann et al., 2007; Fàbregas et al., 2012), and zoos worldwide range from roadside menageries to highly institutionalised 'bioparks' (Robinson, 1992). A study of zoo escapes in Europe revealed that enclosures in zoos, which were members of a regional zoo association, were more secure against animal escape than those that were not members (Fàbregas et al., 2010). In Australia, the ZAA membership consists of over seventy zoos and fauna parks, which is the majority of Australian zoos. These collections range from small family owned fauna parks with native species to large government owned institutions holding a range of native and alien species. Further work is needed to assess if members of a zoo association tend to experience less releases than non-members, and whether institutions experience less releases than fauna parks. Our analyses revealed that zoo releases have increased recently, and this was concomitant, but unrelated, with an increasing number of new zoos (see also Fàbregas et al., 2010). This observed increase is likely to be partly due to the introduction of electronic (definitive) record-keeping versus historical (anecdotal) reporting. Nevertheless, the number of releases has continued to increase throughout the period of electronic record-keeping, and this is not simply due to the increase in the number of reporting zoos (6 new zoos) during this time. Rather, older institutions (opened before 1950) with larger collection sizes (total vertebrate abundance) were more likely to experience a greater number of releases (both escapes and thefts). Larger vertebrate collections do not mean more total species but they do lead to increased opportunities, all else being equal, for stochastic release events. Propagule pressure, the size of the introduction event, is one of the most ubiquitous general drivers underpinning invasion biology (Lockwood et al., 2005, 2009). It is therefore unsurprising that the greater the number of zoo individuals the more likely an escape can, and will, occur.

The fact that larger, older collections are also more targeted for thefts may simply be that these institutions make more visible and attractive targets. There is anecdotal evidence that Australian zoos (including collections that did not partake in our analyses) are professionally targeted for theft, and certain species of small primates (e.g., cotton-top tamarins *Saguinus oedipus*) seem particularly attractive and/or lucrative (Csurshes, 2003). So called 'rational choice' of targets, compared with opportunistic theft, is indeed common in professional larceny (Cornish and Clarke, 2003, 2014). It is, however, surprising that the presence of 24-h security reduced the number of escapes but not the number of thefts, across institutions. One explanation is that while on-site security is effective at discovering (unintentional) breaches from captivity, i.e. before the perimeter fence, it has not been an effective deterrent to intentional (professional) theft. Subsequently, we infer that while escapes from Australian zoos are considerably more frequent than thefts, the smaller number of thefts may also be more difficult to prevent.

Compared with escapes, significantly more reptile thefts occurred than thefts of other vertebrate classes. In particular, more native reptile species were stolen than alien species. Reptiles are highly desired in the live animal market and make up over two-thirds of the international trade in illegal wildlife (Rosen and Smith, 2010). It is possible, that native reptiles are easier to trade in Australia once stolen. The majority of native reptiles are allowed to be kept in private (personal) collections, and in some states you do not require a license to hold native reptiles. In contrast, it is illegal to hold any exotic reptiles in Australia, and all trade is therefore restricted to the black market (Alacs and Georges, 2008). There is indeed a precedent for stolen exotic reptiles in Australia to be

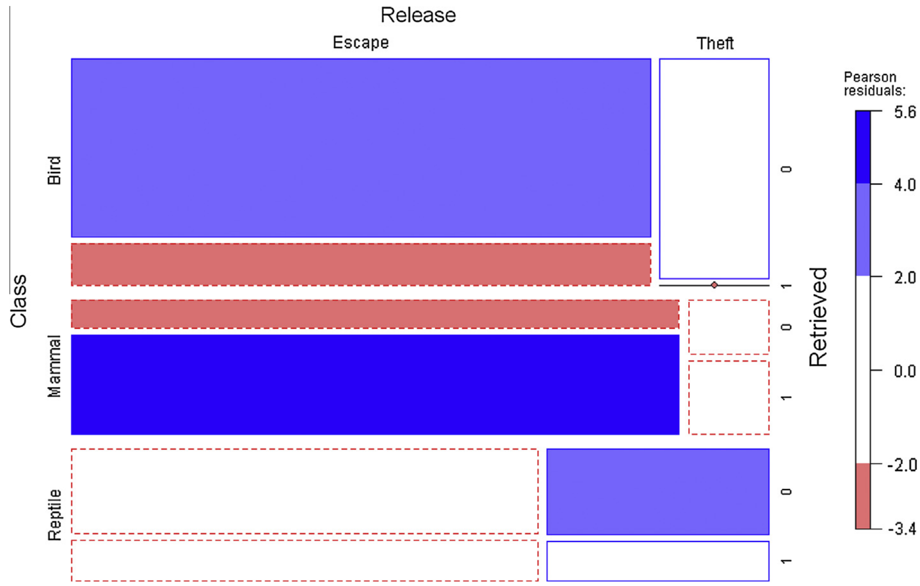

Fig. 4. Mosaic plot of the deviation in conditional independence between release type (escape, theft), taxonomic class (reptile, mammal, bird), and the retrieval outcome (0 = not retrieved, 1 = retrieved) for 220 release events from 19 Australian zoos between 1870 and 2010. The plot is constructed so that the size of each cell (rectangle) is proportional to the observed cell frequency for each trait. The residual-based shading follows Zeileis et al. (2007), and reflects the cell contribution to the Chi-square statistic: shades of blue, when the observed frequency is substantially greater than the expected frequency under independence; shades of red, when the observed frequency is substantially less, as shown in the legend. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

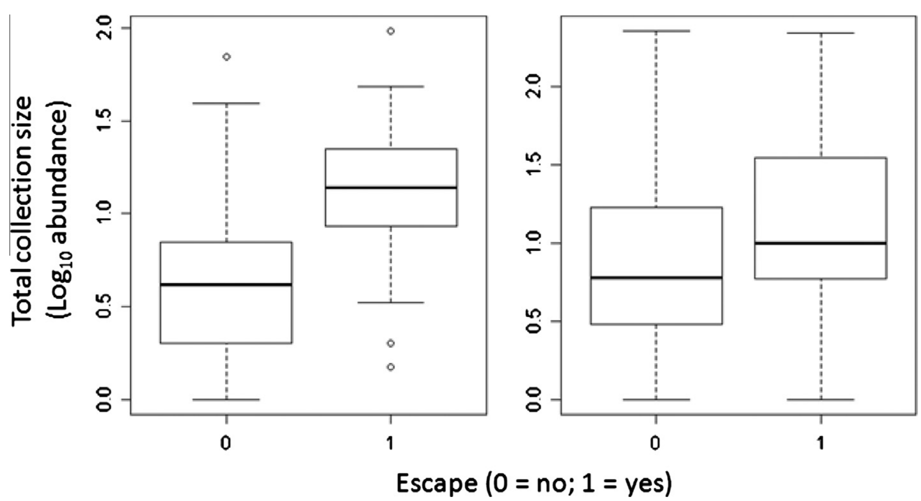

Fig. 5. The significant relationship between average total collection size (Log_{10} abundance) and whether or not a bird species has escaped captivity for (a) 22 bird species escapees since 1990 and (b) all bird species escapes since 1870 (46 species). Current total ZAA collection size was used as a proxy for the size of the holding in (b). Species were more likely to have escaped if their average total collection size was larger.

recovered from (and tracked back to) forums and web pages for the trade in live animals (Garcìa-Dìaz personal communication).

In Europe, similar to the present results, the frequency of vertebrate escapes from zoos was greatest for birds (69%) (Hulme et al., 2008), compared with mammals (29%), and only a single record for amphibians/reptiles. Birds are volant, and highly prone to escaping captivity (Lever, 2005). In addition, birds constitute the largest percentage of vertebrate species held in ISIS zoos (58%), as opposed to mammals (25%), reptiles (11%) and amphibians (6%) (Conde et al., 2013). Bird escapees are known to have high invasion risk, and (outside of Australia) invasive populations have indeed originated from captive escapees (Clergeau and Yésou, 2006). In Australia, the majority of alien bird species are legitimately held in both zoos and private sector collections, both of which have the potential to be a source of alien species incursion. Further investigation into the threats posed by alien bird keeping in the private sector is urgently warranted. The only bird species that has ever escaped from a zoo, and is not also held in private keeping, was a single Chilean flamingo *Phoenicopterus chilensis*, which escaped in 1953. It is believed, that the introduction of double-door aviaries in zoos can reduce the number of bird escapes, but retrieving escaped birds (particularly ones that can readily fly) will always be problematic. We suggest that, in Australia, the general populous may be more capable of determining if a mammal they observe at large is a native species or perhaps a zoo escape, whereas this is more difficult for unfamiliar birds and reptiles. No amphibian, in our dataset (escaped or stolen), was ever retrieved. This is likely due to their comparatively small body-size and cryptic morphology and behaviour, but it is also unknown whether the same effort is invested in retrieving amphibians as for other vertebrates.

Table 3
Model support (ΔAIC; difference in Akaike's Information Criterion) for the top-ranked phylogenetic logistic regression (PLR) models for any bird species ever escaped compared with the Australian holdings for all bird species. Independent variables (median estimates [1st, 99th percentiles]) in the models included: (i) the total current collection size across all zoos; (ii) the species collection type (aviary versus open-range); (iii) the species body mass; and (iv) the species breeding range size. Relative model weights were calculated across the entire model set and sum to one.

Intercept	Log_{10} collection size	Collection type: aviary/open-range	Log_{10} adult body mass	Log_{10} breeding range	Model ranks			ΔAIC	AIC model weights
					1	2	3		
−2.19 [−2.36, −1.49]	0.67 [0.03, 0.81]				87	3	3	0.00 [0.00, 6.01]	0.29 [0.01, 0.37]
−3.36 [−3.69, −3.14]	0.68 [−0.08, 1.06]			0.19 [0.09,0.29]	6	58	8	1.25 [0.00, 7.99]	0.15 [0.00, 0.27]
−2.28 [−2.53, −1.83]	0.70 [0.37, 0.90]	0.20 [−0.36, 0.49]			4	17	48	1.66 [0.00, 3.45]	0.13 [0.05, 0.23]
−1.76 [−2.32, −0.78]	0.67 [0.22, 0.85]		−0.17 [−0.37, −0.01]		2	19	24	1.80 [0.00, 4,23]	0.12 [0.03, 0.24]
−1.53 [−2.03, −1.13]	0.64 [0.39, 0.86]	0.68 [−0.05, 1.00]	−0.34 [−0.50, −0.17]		0	3	14	2.18[0.48, 4.14]	0.10 [0.04, 0.20]
−3.48 [−3.90, −3.30]	0.72 [−0.14, 1.01]		−0.16 [−0.51, −0.02]	0.25 [0.18, 0.43]	1	0	3	2.65 [0.73, 11.8]	0.08 [0.00, 0.10]
−3.46 [−3.80, −3.16]	0.71 [0.32, 1.01]	0.07 [−0.81, 0.49]		0.19 [0.11, 0.27]	0	0	0	3.28 [1.93, 9.01]	0.06 [0.00, 0.10]
−3.30 [−3.87, −2.68]	0.68 [0.34, 0.98]	0.39 [−0.34, 0.86]	−0.23 [−0.55, 0.29]	0.26 [0.07, 0.45]	0	0	0	3.99 [1.72, 51.5]	0.04 [0.00, 0.08]
−0.61 [−0.87, −0.18]		0.82 [0.32, 1.42]	−0.48, [−0.66, −0.35]		0	0	0	5.41 [3.56, 8.61]	0.02 [0.00, 0.04]
−1.65 [−1.81, −1.52]		0.36 [0.07, 0.76]			0	0	0	5.72 [4.00, 8.41]	0.02 [0.01, 0.03]
−0.78 [−1.37, −0.26]			−0.33 [−0.60, −0.09]		0	0	0	6.25 [3.83, 10.1]	0.01 [0.00, 0.03]
−2.82 [−3.50, −1.27]			−0.10 [−0.40, 0.32]	0.32 [0.02, 0.47]	0	0	0	7.79 [5.17, 67.5]	0.00 [0.00, 0.02]
−1.92 [−2.54, −1.57]		0.72 [0.18, 1.76]	−0.33 [−0.78, 0.07]	0.22 [−0.01, 0.38]	0	0	0	10.3 [5.95, 57.5]	0.00 [0.00, 0.01]
−2.84 [−4.33, −2.80]				0.44 [0.18, 0.47]	0	0	0	56.2 [4.67, 66.6]	0.00 [0.00, 0.03]
−2.61 [−4.11, −2.61]		0.24 [−0.52, 0.34]		0.40 [0.17, 0.43]	0	0	0	57.5 [7.32, 65.3]	0.00 [0.00, 0.01]

The vast majority of bird species, which escaped, were reported to have escaped only once. Nevertheless, there are good reasons to assume that propensity for a species to escape may be both species-specific and correlated with traits (life-history, behavioural, ecological) that are phylogenetically conserved, i.e., shared among related species. Only two bird species (the native Raja shelduck *Tadorna radjah* and the alien Indian ringneck parrot *Psittacula krameri*) have escaped zoo captivity more than five times since 1870. The Indian ringneck is also the most frequent bird incursion from private backyard keeping in Australia (Henderson et al., 2011). Regardless, there was only weak evidence of phylogenetic signal in a species' propensity to escape (versus species not recorded to escape) for recent escapees (since 1990; $n = 22$ species), and no evidence of phylogenetic signal for all reported escapees ($n = 46$ species). In fact, the only consistent variable associated with bird species escaping was the size of the collection, or holding. Simply put, the more individuals of a species held, either in a single zoo collection or summed across all zoos, the more likely a species was to have escaped. This was unrelated to whether, or not, species are held in aviaries or open-yards and ponds. Clearly, the role of propagule pressure for (stochastic) avian escapes from zoos is as important as it is in driving the natural colonisation (Cassey and Blackburn, 2004) and alien introduction (Cassey et al., 2004) of bird species.

Zoos are a prominent part of our culture and play a valuable role in educating the public in conservation issues (Beri et al., 2010). The World Zoo and Aquarium Association Conservation Strategy, which governs all WAZA members (including those zoos in Australia) requires that zoos and aquariums undertake every effort to prevent the escape of animals and plants of alien invasive species (WAZA, 2005). Furthermore, the EU Zoo Animals Directive relating to the keeping of wild animals in zoos places a responsibility for 'preventing the escape of animals in order to avoid possible ecological threats to indigenous species and preventing intrusion of outside pests and vermin' (Miller et al., 2006). There is recognition that zoos pose an invasion pathway risk and as a result the Australian zoo industry is working towards mitigating this risk. Part of this mitigation is ensuring ZAA members undertake every effort to prevent escapes and thefts, and that institutions are required to meet industry benchmarks before joining the ZAA. We strongly recommend that this same risk mitigation and vigilance should be applied to other licensed holders of alien fauna, to ensure that the risk pathway across all potential holders of alien species is reduced.

5. Conclusion

In Australia, many alien vertebrate species are maintained in private (i.e., personal backyard) collections (birds and fish), or traded illegally (reptiles and amphibians). These collections are the frequent (and increasing) source for incursions of new vertebrates at large in the wild (Henderson et al., 2011). National coordination of data, collected on the releases of alien species from both public and private keeping, as well as data sharing among government agencies and industry partners, would allow subsequent analyses to identify the relative contribution (scale and type) of these biosecurity incursion risks. ZAA members generally manage large collections, which are industry supported and well-maintained, and as a result may pose a low risk for biological invasion compared to unregulated collections. In Australia, we conclude that the establishment risk of alien vertebrate species from zoo collections is low, and substantially less than other 'backyard' and illegal sources of alien species keeping and trade (Alacs and Georges, 2008; Henderson et al., 2011).

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2014.10.023.

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