

PATTERNS OF COCCIDIAL PREVALENCE IN LIZARDS OF MAURITIUS

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ABSTRACT: This paper reports prevalence of coccidial oocysts in fecal samples from 6 endemic and 2 introduced lizard species on Mauritius, an island nation in the Indian Ocean. Total coccidial prevalence was 54% ($n = 341$) for the endemic 'ornate day gecko,' *Phelsuma ornata*; 48% ($n = 159$) for the endemic 'Durrell's night gecko,' *Nactus durrelli*; 53% ($n = 15$) for the endemic 'Serpent Island night gecko,' *N. serpensinsula*; and 78% ($n = 248$) for the introduced gecko, *Hemidactylus frenatus*. These high prevalences may reflect lack of long-lasting immune response to coccidial infection. There were few significant differences in prevalence among age, island, sex, or body condition within species, suggesting that these coccidia are relatively nonpathogenic and have little effect on host fitness. Prevalence was higher in the dry season than the wet season. These data suggest other factors, such as low host immune response to reinfection, affect overall prevalence more significantly than the effect of humidity on oocyst survival on Mauritius. No coccidia were found in samples from the endemic 'Gunner's Quoin night gecko,' *N. coindemirensis* ($n = 155$), probably reflecting parasite extinction due to a host population bottleneck following historical introduction of rats. There was no evidence of competitive or facilitative interactions between *Eimeria* sp. and *Isoospora* sp., but evidence of competition between 2 *Eimeria* species in the 'ornate day gecko,' *Phelsuma ornata*. No evidence was found of cross-species infection, suggesting that reptile coccidia have high host specificity and are, therefore, poor subjects for studies of parasite-mediated competition and the evolution of sex.

Coccidial infections have been reported from a wide range of animals, including mammals, birds, reptiles, amphibians, and invertebrates (Levine, 1988). However, little is known about the ecology and impact of coccidia on host populations except for domestic poultry, sheep, and cattle (Hammond and Long, 1973). In these animals, coccidia often cause pathogenic infections, leading to economic loss and sometimes high mortality (Long, 1973; Fernando, 1982). In contrast, consistently high prevalence and intensity of coccidial infection in some small mammals occur without apparent clinical signs of infection (Dorney, 1963; Seville et al., 1992, 1996; Spurgin and Hnida, 2002). This has led authors to suggest that some coccidians may have no significant pathological effect on the host, even though they infect and kill host cells in the gastrointestinal (GI) tract and other organs they inhabit (Seville et al., 1996).

A range of biotic and abiotic factors may affect the prevalence of directly transmitted parasites within a host population. These include host population density, age structure, behavior, immune status, and sex, as well as climate, weather, ultraviolet radiation, and others (Long, 1973; Ovezmukhammedov, 1974; Dobson et al., 1992; Couch et al., 1993; Daszak, 1995). In island species, host density may be higher than in mainland species due to the depauperate nature of the fauna (Rodda and Dean-Bradley, 2002). This may lead to higher prevalence for parasites that are transmitted in a density-dependent manner (Goldberg and Bursey, 1990). Abiotic factors such as humidity may also affect the external oocyst stage of coccidians and may be important in explaining prevalence for island species (Daszak, 1995). In this paper, patterns of coccidial prevalence in a large number of fecal samples ($n = 1,083$) from native and introduced lizards of Mauritius are reported. Abiotic and biotic factors that may influence prevalence are discussed, as well as the potential use of this system for studies of apparent com-

petition between native and introduced hosts, and competitive exclusion or facilitation between parasite species.

MATERIALS AND METHODS

Coccidial survey

Fecal samples were collected between February and December 2003, from 5 endemic reptile species and 2 introduced reptile species from mainland Mauritius and 7 islands surrounding Mauritius (Fig. 1, Table I). Due to logistical limitations, islands were visited only in the months listed in Table I, such that some islands were visited in some months and other islands in other months. Lizards were captured by hand and placed in cloth bags overnight and subsequently released at the site of capture. Fecal samples were removed, placed in Eppendorf tubes with 2 ml of 2.5% aqueous potassium dichromate to allow sporulation of coccidial oocysts, and stored at ambient temperature. Samples were examined by wet mounts of fecal suspensions on a Nikon Epsom 2000 microscope (Nikon Inc., Melville, New York) and photographed using a Zeiss Photomicroscope III (Carl Zeiss, Inc., Thornwood, New York). To ensure consistency, all samples were examined by placing approximately 0.1 ml of the fecal suspension and a 22×30 mm coverslip on each slide. Twenty-five fields of view were examined at $\times 25$ magnification to determine whether the sample was positive for oocysts. Up to 5 oocysts from each coccidian species in positive samples were measured under oil at $\times 100$. These measurements were morphologically compared to the coccidia already described from the 2 introduced species that we studied on Mauritius, *Hemidactylus frenatus* and *Calotes versicolor*, to coccidia from *Phelsuma* sp. day geckoes (McAllister et al., 1990; Daszak and Ball, 1991; Upton et al., 1991, 1994; Ball and Daszak, 1995; Daszak, 1995; Finkelman and Paperna, 1995; Hanley et al., 1995; Modry et al., 1997; Saum et al., 1997) and to 14 coccidia species that are awaiting description (S. J. Ball and P. Daszak, unpubl. obs.). We discovered 2 additional new species and measured 30 oocysts of each, took photomicrographs, and will describe these in a separate publication.

Statistical analyses

Prevalence of the most common eimerian in each host species was compared between sexes, islands, and month of collection using chi-square or Fisher's exact tests. We tested for correlations between the infection status of a lizard and its size, measured by snout-to-vent length (SVL), using binary logistic regression (SVL was used as a surrogate for the age of individuals). Binary logistic regression was used to test for a relationship between the body condition of a lizard and its infection status. An index of body condition was generated for each lizard by regressing mass on SVL and retaining the residual (Petren and Case, 1996). Finally, chi-square contingency tests were used to examine the possibility of interaction between parasite species. These tests deter-

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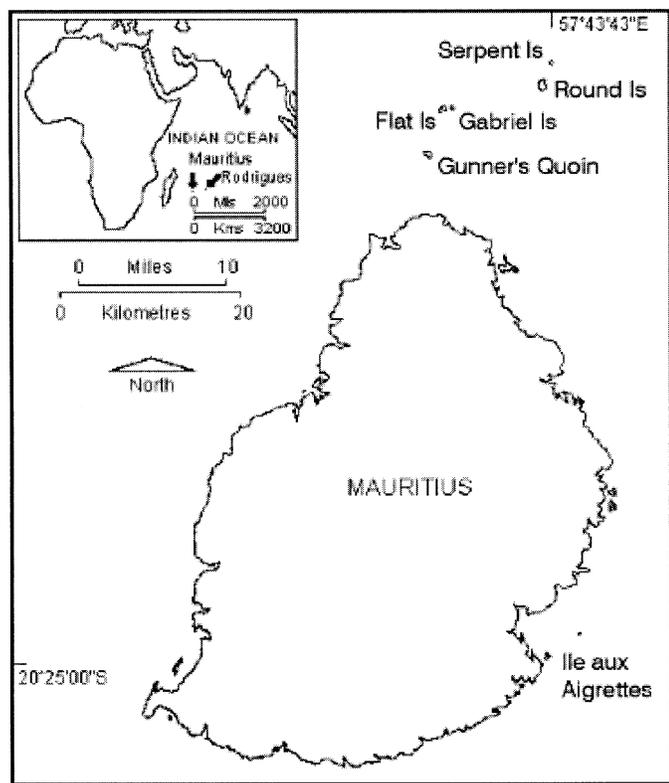


FIGURE 1. Map of Mauritius and its offshore islands. Ile aux Fouquets and Ile de la Passe are represented as a point approximately 3 miles NE of Ile aux Aigrettes.

mined whether there were more or less multiple infections than expected, which would be suggestive of facilitative or competitive interactions. Chi-squared (χ^2) values and, for *t*-tests, *t*-values are given in the results.

To determine whether or not samples of different sexes, islands, or collecting periods could be combined, analyses were performed in the following order: month of capture, island, and sex. Data were combined for subsequent analyses when the groups appeared to be unambiguously similar ($P > 0.5$) and where groups of samples were collected in adjacent months. We did not perform season, island, and sex analyses for isosporan coccidia because of insufficient sample sizes given the low prevalences for this genus. For each analysis, the sex, islands, and months of capture that were used in the analysis are given using abbreviations given in Table I. Meteorological data were supplied by Mauritius Meteorological Services (<http://ncb.intnet.mu/meteo.htm>).

RESULTS

A total of 1,083 fecal samples was collected from 7 islands surrounding Mauritius, representing 8 species of reptile (Table I). The majority of the coccidian oocysts were morphologically similar to those found previously from Round Island reptiles (Daszak, 1995) but not yet described. Two other previously undescribed coccidia were also found in samples from the endemic 'ornate day gecko,' *P. ornata* (an *Isospora* sp.); and from the endemic 'Serpent Island night gecko,' *Nactus serpensinsula* (an *Eimeria* sp.). *Adelina* sp. coccidia were observed in a number of samples collected. The oocysts observed are consistent with an *Adelina* species from Round Island centipedes (*Scolopendra abnormis*) (P. Daszak, unpubl. obs.). Because it is likely that the presence of *Adelina* sp. oocysts is a result of eating prey infected with *Adelina* sp. and does not represent an active

infection (Daszak, 1995), *Adelina* species were not included in the analyses.

No coccidia were observed in samples collected from the endemic skink, *Gongylomorphus fontenayi*, on Flat Island ($n = 10$); the endemic night gecko, *Nactus coindemirensis* ($n = 155$) on Gunner's Quoin ($n = 146$); or the undescribed, endemic species of *Nactus* gecko on Flat Island ($n = 9$). A single sample collected from the introduced agamid lizard, *Calotes versicolor*, was found to be positive for coccidia.

Table I shows the prevalence of coccidial infections for 4 host species that we studied in detail by island of origin and month of capture. Overall, coccidial prevalence was 54% ($n = 341$) for the endemic 'ornate day gecko,' *P. ornata*; 48% ($n = 159$) for the endemic 'Durrell's night gecko,' *Nactus durrelli*; 53% ($n = 15$) for the endemic 'Serpent Island Gecko,' *N. serpensinsula*; and 78% ($n = 248$) for the introduced *H. frenatus*. In all lizards, the more common *Eimeria* species was more prevalent than any *Isospora* species (Table I).

Month of sample collection

Eimeria dobsoni infection prevalence in *P. ornata* was found to be significantly lower in samples collected from males in March (10/25) than in July (14/20) from Gunner's Quoin (Table I; $\chi^2 = 4.02$, $P = 0.045$). Similarly, coccidial prevalence was lower in *H. frenatus* samples collected from males in March (12/24) than those collected in June (14/19) from Ile de la Passe. However, this difference was not statistically significant ($\chi^2 = 2.49$, $P = 0.12$). Based on these comparisons we did not combine data from samples collected in February–April with those collected in May–July.

Host island of origin

For *P. ornata* there was no significant difference between islands comparing data from males from GQ-3, FI-4, and IAA-2 (see Table I for abbreviations; $\chi^2 = 0.31$, $P = 0.86$); from RI-5 and GQ-7 ($\chi^2 = 0.02$, $P = 0.90$); and from females from GQ-3, FI-4, and IAA-3 ($\chi^2 = 1.9$, $P = 0.39$). Similarly, there was no significant difference between islands for *H. frenatus* in 2 separate comparisons with males (IAF-5 [12/19] vs. DLP-6 [14/19], $\chi^2 = 0.49$, $P = 0.49$ and DLP-3 [12/24] vs. IAA-2 [21/48], $\chi^2 = 0.25$, $P = 0.62$) and 2 comparisons with females (IAA-4 [24/31] vs. FI-4 [17/26], $\chi^2 = 1.01$, $P = 0.36$ and IAF-5 [24/28] vs. DLP-6 [22/24], $\chi^2 = 0.45$, $P = 0.50$).

Sex of host

In *P. ornata*, the prevalence of males (22/61) was marginally higher than of females (7/38) in March and April, (FI-4 and GQ-3 combined; $\chi^2 = 3.52$, $P = 0.061$), but not in May (males, 15/22; females, 14/22; $\chi^2 = 0.10$, $P = 0.75$) when overall prevalences were higher. In *H. frenatus*, male prevalence was lower (26/38) than female prevalence (46/52; DLP-6 and IAF-5 combined, $\chi^2 = 5.51$, $P = 0.019$). In contrast, in *N. durrelli* there was no difference in prevalence between male prevalence (35/86) and female prevalence (27/63; $\chi^2 = 0.07$, $P = 0.79$). Finally, for *N. serpensinsula*, male prevalence (4/10) was less than female prevalence, (4/5), but this difference was not significant (Fisher's exact test, $P = 0.28$).

TABLE I. Prevalence of *Eimeria* and *Isospora* in 4 types of geckoes (Gekkonidae) on 7 islands near Mauritius, 2003.* Prevalence from multiple visits to islands are presented separately following the island average.

| Host species, common name, island of origin, and endemic status | No. of samples, (month collected) | Coccidia species | | |
|--|-----------------------------------|--------------------|----------------------|-----------------------|
| <i>Phelsuma ornata</i> 'Ornate day gecko' (endemic) | | <i>E. dobsoni</i> | <i>E. brianbelli</i> | <i>I. bullocki</i> |
| All islands and dates | 405 | 43% | 15% | 14% |
| Flat Island (FI)† | 55 (4) | 62% | 22% | 27% |
| Gunner's Quoin (GQ) | 64 (3, 7‡) | 44% | 44% | 16% |
| March visit | 44 (3) | 32% | 7% | 14% |
| July visit | 20 (7‡) | 70% | 5% | 20% |
| Ile aux Aigrettes (IAA) | 89 (2‡, 3§) | 31% | 9% | 0% |
| February visit | 58 (2‡) | 31% | 9% | 0% |
| March visit | 31 (3§) | 32% | 10% | 0% |
| Round Island (RI) | 44 (5) | 66% | 5% | 45% |
| <i>Hemidactylus frenatus</i> 'Common house gecko' introduced | | <i>E. furmani</i> | <i>I. schlegeli</i> | <i>I. cunninghami</i> |
| All islands and dates | 394 | 69% | 14% | 7% |
| Flat Island | 55 (4) | 65% | 15% | 5% |
| Ile aux Aigrettes | 79 (2‡, 4§) | 65% | 22% | 2.4% |
| February visit | 48 (2‡) | 56% | 17% | 0% |
| April visit | 31 (4§) | 77% | 29% | 6% |
| Ile aux Fouquets (IAF) | 47 (5) | 77% | 0% | 4% |
| Ile de la Passe (DLP) | 67 (3‡, 6) | 72% | 10% | 15% |
| March visit | 24 (3‡) | 50% | 13% | 4% |
| June visit | 43 (6) | 84% | 9% | 21% |
| <i>Nactus durrelli</i> 'Durrell's night gecko' (endemic) | | <i>E. mungrooi</i> | <i>I. bloxami</i> | |
| Round Island | 159 (5) | 40% | 15% | |
| <i>Nactus serpentsinsula</i> 'Serpent Island night gecko' (introduced) | | <i>E. mungrooi</i> | <i>I. bloxami</i> | <i>E. leinwandi</i> |
| Serpent Island (SI) | 15 (11) | 20% | 40% | 13% |

*No coccidia were observed in fecal samples from the endemic skink, *Gongylomorphus fontenayi*, on Flat Island (n = 10); the endemic 'Gunner's Quoin night gecko,' *Nactus coindemirensis* (n = 155), on Gunner's Quoin (n = 146); or the undescribed, endemic species of *Nactus* night gecko on Flat Island (n = 9). A single sample collected from the introduced agamid *Calotes versicolor* was found to be positive for a new species of coccidian.

†*I. northi* was found in a single individual of this species for a prevalence of 18%.

‡Samples from males only.

§All samples from females only.

Age of host

A binary logistic regression of infection status vs. age measured by log-transformed SVL showed marginally significant positive coefficients for *H. frenatus* (FI-4: coefficient = 15.989; N = 55; T = 2.15; P = 0.031, and IAF-5 and DLP-6 (with sex as the covariate): coefficient = 14.083; N = 90; T = 1.91; P = 0.057), but not for *P. ornata* (RI-5 and GQ-7 (N = 65) and GQ-3 and FI-4 and IAA-3 (N = 188), both with sex as the covariate: both P values >0.3, or *N. durrelli* (RI-5: coefficient = 4.55; N = 159; T = 1.84; P = 0.066). Other sets of samples were too small for adequate testing.

Body condition

There were no significant relationships between infection status and host body condition for *P. ornata* (5 comparisons), *H. frenatus* (2 comparisons), or *N. durrelli* (1 comparison; all P values >0.27).

Parasite interactions

In *P. ornata* from IAA, there was strong evidence for competition between *Eimeria brianbelli* and *Eimeria dobsoni* (February, males, $\chi^2 = 14.98$, P < 0.001; March, females, $\chi^2 = 9.16$,

P < 0.005). In other species, there was no evidence of competition or facilitation between the most prevalent *Eimeria* species and *Isospora* species in *N. durrelli*, *P. ornata*, or *H. frenatus* (7 comparisons, all P values >0.25).

DISCUSSION

The coccidia of the lizards of Mauritius and its surrounding islands provide an ideal subject to study island parasite ecology. Each reptile species apparently has endemic coccidia, and populations on different islands are effectively cut off from other conspecific populations. The possibility of migration between populations is significantly impeded by the constant trade winds and high seas throughout the winter and the large distances between islands (Fig. 1). In our study, there was no evidence of coccidial transmission or cross-infection between any of the 7 species studied here, including the introduced invasive 'common house gecko,' *H. frenatus*. The data from Mauritian geckoes suggest that their coccidia are not infectious for each other, consistent with the strict host specificity reported for most reptile coccidia, including those in sympatric geckoes (Levine, 1988; Bannert, 1994; Ball and Daszak, 1995).

This study demonstrates that populations of endemic and introduced lizards of Mauritius have consistently high prevalences

es of coccidia. Similar high prevalences have been reported previously from reptiles of Mauritius, of other tropical islands, and of nonarid tropical regions (Daszak, 1995; Couch et al., 1996). In addition, a histological survey of tissue for coccidia from a population of island-inhabiting lizard revealed higher prevalence of coccidial infection than those reported here (Goldberg and Bursey, 1990). One possible explanation for the lower coccidian prevalence in feces is because oocysts are not shed in feces throughout the entire endogenous life cycle of coccidia and oocyst shedding can vary diurnally (Levine, 1942; Levine, 1982; Brawner and G.E., 1999; Brown et al., 2001). For some species, oocysts of coccidia are shed for 50% or less of the entire infectious period. Therefore, it is possible that coccidial prevalences of 50% or higher represent almost continual reinfection of individuals (Ball and Lewis, 1984). The high prevalences reported here suggests that that Mauritian reptiles are either chronically infected or continually reinfected with their most common coccidian (normally an *Eimeria* species).

Persistent high prevalence has been reported for reptile blood parasites (Sorci, 1995), reptile helminths (Bursey and Goldberg, 1994), and for many rodent coccidia (Dorney, 1963, 1966; Ball and Lewis, 1984; Stanton et al., 1992; Thomas et al., 1995; Fuller, 1996; Seville et al., 1996; Higgs and Nowell, 2000; Bertolino et al., 2003). Some authors have suggested that this indicates coccidia are nonpathogenic in these populations and that they have a minimal effect on host fitness. However, this pattern could also be explained by a pathogenic parasite that does not elicit a lasting acquired immune response, and either chronically infects hosts, or rapidly reinfests hosts after the infection is cleared. Infectious agents that elicit a strong, lasting immune response should be less prevalent in older animals, because these are more likely to have already been infected and become immune to infection. This pattern was observed for coccidial parasites of the mouse *Peromyscus maniculatus* (Fuller, 1996). In the current study, regression analyses showed weak or non-significant positive correlations between prevalence and age, suggesting that these coccidia do not elicit a lasting immune response. The lack of correlation between prevalence and host body condition also may suggest that these coccidia are nonpathogenic in Mauritian lizards. This finding agrees with ecological and nutritional studies of some small mammals, which concluded that their coccidia are relatively nonpathogenic (Ball and Lewis, 1984; Seville et al., 1992, 1996). Conversely, a study of *P. maniculatus* found that coccidial infection correlated with decreased host survival despite lack of correlation with body condition (Fuller and Blaustein, 1996). This may be a result of infected animals foraging for longer periods of time, which allows them to maintain good body condition, but exposes them to additional predation, as may be the case with Mauritian lizards.

Previous analyses have shown that low environmental humidity is a predictor for low coccidial prevalence in reptile populations because transmission occurs through an external oocyst stage, which is susceptible to desiccation (Ovezmukhamedov, 1974; Daszak, 1995). In the current study, the prevalence of coccidia in Mauritian reptiles was actually higher in the cool and dry season from May to October than in the warm and wet season from November to April. Throughout Mauritius, mean humidity remains higher than 70% throughout

the year. These data suggest other factors (e.g., low host immune response to reinfection) affect overall prevalence more significantly than the effect of humidity on oocyst survival. However, it is important to note that interpretation of seasonal data may be confounded by recruitment or other temporally varying factors.

Significant differences in coccidian prevalence between sexes were observed only in certain seasons, and this differed between host species. Other studies of island reptile coccidia found no significant difference in prevalence between sexes (Goldberg and Bursey, 1990; Couch et al., 1996). Within rodents, differences in coccidial prevalence between sexes (or female reproductive state) have been reported in some species (Ball and Lewis, 1984; Bertolino et al., 2003), but not in others (Higgs and Nowell, 2000). The differences in prevalence found between sexes in the current study may reflect differences in space-use patterns and social organization of males and females, which may be different between species, habitats, and classes (Bertolino et al., 2003).

There was no evidence of competition or facilitation between *Eimeria* spp. and *Isoospora* spp. in any of the reptiles studied. In Galapagos reptiles, *Eimeria* spp. were the most prevalent coccidians and it was hypothesized that this is due to competition between coccidial genera (Couch et al., 1996). Species of *Eimeria* are also the most prevalent in Mauritian reptiles, but our analyses suggest that competition is not the cause. We did find strong evidence for competition between *Eimeria brianbelli* and *Eimeria dobsoni* in samples from the endemic 'ornate day gecko,' *P. ornata*, from IAA. Both *E. brianbelli* and *E. dobsoni* have subspherical oocysts, a common trait of intestinal coccidia, rather than gall bladder coccidians, which are often cylindrical in reptiles (Paperna and Landsberg, 1989). Although *Isoospora* spp. and *Eimeria* spp. are often found in similar regions of the GI tract, it may be more likely that 2 eimerians would inhabit similar cells, and thus compete. A histological study that examined the exact location in the GI tract of each species infection would test this hypothesis.

No coccidia were found in fecal samples of the endemic 'Gunner's Quoin night gecko,' *N. coindemirensis*, from Gunner's Quoin ($n = 146$), and the undescribed endemic *Nactus* sp. night gecko from Flat Island ($n = 9$). Its 2 sister taxa, the 'Serpent Island gecko' (*N. serpensinsula*) and 'Durrell's night gecko' (*N. durrelli*) share an *Isoospora* and an *Eimeria* species with prevalences between 20% and 40% (Table I). The lack of coccidia in the Flat Island samples may be due to the small sample size, but the absence of oocysts in the much larger sample size from Gunner's Quoin suggests this *N. coindemirensis* night gecko population may be coccidia-free. Introduced species often have lower parasite biodiversity than their conspecifics in the country of origin due to the usually small size of the founding colony (Mitchell and Power, 2003; Torchin et al., 2003). However, it is unlikely that a founder effect explains these data because Gunner's Quoin and the other outer islands rest on a submarine shelf that was exposed during Quaternary sea level falls (Arnold, 1980). During the last glaciation (around 13,000–7,000 yr B.P.) 'Durrell's night gecko' (*N. durrelli*) and the 'Gunner's Quoin night gecko' (*N. coindemirensis*) were almost certainly sympatric, with their current distribution explained by competitive exclusion or competition from introduced 'common house gecko' (*H. frenatus*) (Arnold, 1980; Ar-

nold and Jones, 1994). It is therefore more likely that the lack of coccidia in the 'Gunner's Quoin night gecko' (*N. coindemirensis*) on Gunner's Quoin is due to a severe population bottleneck caused by predation from the introduced brown rat, *Rattus norvegicus* (Bell, 2002). Such a bottleneck may have reduced the host population below the threshold density for coccidian transmission (McCallum and Dobson, 1995) and led to extinction of their coccidia.

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LITERATURE CITED

- ARNOLD, E. N. 1980. Recently extinct reptile populations from Mauritius and Reunion, Indian Ocean. *Journal of Zoology* **191**: 33–47.
- , AND C. G. JONES. 1994. The night geckos of the genus *Nactus* in the Mascarene islands with a description of the distinctive population on Round Island. *Dodo. Journal of the Wildlife Preservation Trusts* **30**: 119–131.
- BALL, S. J., AND P. DASZAK. 1995. Description of the oocysts of three new species of *Eimeria* (Apicomplexa, Eimeriidae) from geckoes (Sauria, Gekkonidae). *Systematic Parasitology* **32**: 101–106.
- , AND D. C. LEWIS. 1984. *Eimeria* (Protozoa: Coccidia) in wild populations of some British rodents. *Journal of Zoology* **202**: 373–381.
- BANNERT, B. 1994. Investigations on the host-specificity of *Dihomonous sarcosporidia* in the intermediate and definitive host. *Journal of Eukaryotic Microbiology* **41**: 183–188.
- BELL, B. D. 2002. The eradication of alien mammals from five offshore islands, Mauritius, Indian Ocean. In *Turning the tide: The eradication of invasive species*, C. R. Veitch and M. N. Clout (eds.). IUCN, Gland, Switzerland, p. 40–45.
- BERTOLINO, S., L. A. WAUTERS, L. DE BRUYN, AND G. CANESTRI-TROTTI. 2003. Prevalence of coccidia parasites (Protozoa) in red squirrels (*Sciurus vulgaris*): Effects of host phenotype and environmental factors. *Oecologia* **137**: 286–295.
- BRAWNER, W. R., AND H. G. E. 1999. Temporal variation in shedding of coccidian oocysts: Implications for sexual selection. *Canadian Journal of Zoology* **77**: 347–350.
- BROWN, M. A., S. J. BALL, AND D. HOLMAN. 2001. The periodicity of isosporan oocyst discharge in the greenfinch (*Carduelis chloris*). *Journal of Natural History* **35**: 945–948.
- BURSEY, C. R., AND S. R. GOLDBERG. 1994. Persistence of the component parasite community of Yarrow's spiny lizard, *Sceloporus jarrovi*, 1967–1991. *Journal of the Helminthological Society of Washington* **61**: 141–145.
- COUCH, L., D. W. DUSZYNSKI, AND E. NEVO. 1993. Coccidia (Apicomplexa), genetic diversity, and environmental unpredictability of four chromosomal species of the subterranean superspecies *Spalax ehrenbergi* (mole rat) in Israel. *Journal of Parasitology* **79**: 181–189.
- , P. A. STONE, D. W. DUSZYNSKI, H. L. SNELL, AND H. M. SNELL. 1996. A survey of the coccidian parasites of reptiles from islands of the Galapagos archipelago: 1990–1994. *Journal of Parasitology* **82**: 432–437.
- DASZAK, P. 1995. Prevalence of endoparasites in Round Island reptiles. *Herpetological Journal* **5**: 195–199.
- , AND S. J. BALL. 1991. Five new species of *Eimeria* (Apicomplexa, Eimeriidae) from lizards. *Systematic Parasitology* **20**: 141–147.
- DOBSON, A. P., S. V. PACALA, J. D. ROUGHGARDEN, E. R. CARPER, AND E. A. HARRIS. 1992. The parasites of *Anolis* lizards in the Northern Lesser Antilles. 1. Patterns of distribution and abundance. *Oecologia* **91**: 110–117.
- DORNEY, R. S. 1963. Coccidiosis—Incidence, epizootiology in two Wisconsin Sciuridae. *North American Wildlife Natural Resources Conference* **28**: 207–215.
- . 1966. Quantitative data on four species of *Eimeria* in eastern chipmunks and red squirrels. *Journal of Protozoology* **13**: 549–550.
- FERNANDO, M. A. 1982. Pathology and pathogenicity. In *The biology of the coccidia*, P. L. Long (ed.). University Park Press, Baltimore, Maryland, p. 287–327.
- FINKELMAN, S., AND I. PAPERNA. 1995. The endogenous development of 2 new species of *Isospora* Schneider, 1881 (Apicomplexa, Eimeriidae) from Thai geckoes. *Systematic Parasitology* **30**: 213–221.
- FULLER, C. A. 1996. Population dynamics of two species of *Eimeria* (Apicomplexa: Eimeriidae) in deer mice (*Peromyscus maniculatus*): Biotic and abiotic factors. *Journal of Parasitology* **82**: 220–225.
- , AND A. R. BLAUSTEIN. 1996. Effects of the parasite *Eimeria arizonensis* on survival of deer mice (*Peromyscus maniculatus*). *Ecology* **77**: 2196–2202.
- GOLDBERG, S. R., AND C. R. BURSEY. 1990. Prevalence of *Eimeria noctisauris* (Apicomplexa: Eimeriidae) in the island night lizard, *Xantusia riversiana* (Xantusiidae). *Journal of Herpetology* **24**: 204–207.
- HAMMOND, D. M., AND P. L. LONG. 1973. *The coccidia*. University Park Press, Baltimore, Maryland, 482 p.
- HANLEY, K. A., D. M. VOLLMER, AND T. J. CASE. 1995. The distribution and prevalence of helminths, coccidia and blood parasites in two competing species of gecko—Implications for apparent competition. *Oecologia* **102**: 220–229.
- HIGGS, S., AND F. NOWELL. 2000. Population biology of *Eimeria* (Protozoa: Apicomplexa) in *Apodemus sylvaticus*: A capture/recapture study. *Parasitology* **120**: 355–363.
- LEVINE, N. D. 1982. Taxonomy and life cycles of coccidia. In *The Biology of the Coccidia*, P. L. Long (ed.). University Park Press, Baltimore, Maryland, p. 9–20.
- . 1988. *The protozoan phylum Apicomplexa*. CRC Press, Boca Raton, Florida, 351 p.
- LEVINE, P. P. 1942. The periodicity of oocyst discharge in coccidial infection of chickens. *Journal of Parasitology* **28**: 346–348.
- LONG, P. L. 1973. Pathology and pathogenicity of coccidial infections. In *The Coccidia*, D. M. Hammond and P. L. Long (eds.). University Park Press, London, U.K., p. 253–294.
- MCCALLISTER, C. T., S. J. UPTON, AND D. M. BOYER. 1990. *Eimeria dixoni* sp.n. (Apicomplexa, Eimeriidae) from an introduced population of common house geckos, *Hemidactylus frenatus* (Sauria, Gekkonidae), in Dallas County, Texas. *Journal of the Helminthological Society of Washington* **57**: 1–4.
- MCCALLUM, H., AND A. DOBSON. 1995. Detecting disease and parasite threats to endangered species and ecosystems. *Trends in Ecology and Evolution* **10**: 190–194.
- MITCHELL, C. E., AND A. G. POWER. 2003. Release of invasive plants from fungal and viral pathogens. *Nature* **421**: 625–627.
- MODRY, D., B. KOUDELA, AND J. VOLF. 1997. Four new species of *Isospora* Schneider, 1881 (Apicomplexa: Eimeriidae) from reptiles from the islands of Seychelles. *Systematic Parasitology* **37**: 73–78.
- OVEZMUKHAMMEDOV, A. 1974. Ecological data on intestinal coccidia parasitising reptiles of Turkmenistan. *Izvestia Akademi Nauk Turkmenkoi SSR. Seriya Biologicheskik Nauk* **5**: 64–67.
- PAPERNA, I., AND J. H. LANDSBERG. 1989. Description and taxonomic discussion of eimerian coccidia from African and Levantine geckoes. *South African Journal of Zoology* **24**: 345–355.
- PETREN, K., AND T. J. CASE. 1996. An experimental demonstration of exploitation competition in an ongoing invasion. *Ecology* **77**: 118–132.
- RODDA, G. H., AND K. DEAN-BRADLEY. 2002. Excess density compensation of island herpetofaunal assemblages. *Journal of Biogeography* **29**: 623–632.
- SAUM, L. P., C. H. DIONG, AND T. E. MCQUISTON. 1997. *Isospora lacertae*: A new coccidian parasite (Apicomplexa: Eimeriidae) from the oriental garden lizard, *Calotes versicolor* (Squamata: Agamidae) from Singapore. *Acta Protozoologica* **36**: 143–145.
- SEVILLE, R. S., H. J. HARLOW, N. L. STANTON, AND M. L. WAGNER. 1992. Effects of eimerian (Apicomplexa: Eimeriidae) infections on nutrient assimilation in the Wyoming ground squirrel. *Journal of Parasitology* **78**: 881–885.

- , N. L. STANTON, AND K. GEROW. 1996. Stable parasite guilds: Coccidia in spermophiline rodents. *Oikos* **75**: 365–372.
- SORCI, G. 1995. Repeated measurements of blood parasite levels reveal limited ability for host recovery in the common lizard (*Lacerta vivipara*). *Journal of Parasitology* **81**: 825–827.
- SPURGIN, R. J., AND J. A. HNIDA. 2002. *Eimeria lancasterensis* and *Eimeria ontarioensis* from fox squirrels, *Sciurus niger*, in southeastern Nebraska, USA. *Comparative Parasitology* **69**: 211–212.
- STANTON, N. L., L. M. SHULTS, M. PARKER, AND R. S. SEVILLE. 1992. Coccidian assemblages in the Wyoming ground squirrel, *Spermophilus elegans elegans*. *Journal of Parasitology* **78**: 323–328.
- THOMAS, D. M., N. L. STANTON, AND R. S. SEVILLE. 1995. A stable Eimerian assemblage in Wyoming ground-squirrels (*Spermophilus Elegans Elegans*)—Maintaining viability over winter. *Journal of the Helminthological Society of Washington* **62**: 1–5.
- TORCHIN, M. E., K. D. LAFFERTY, A. P. DOBSON, V. J. MCKENZIE, AND A. M. KURIS. 2003. Introduced species and their missing parasites. *Nature* **421**: 628–630.
- UPTON, S. J., K. HANLEY, AND T. J. CASE. 1994. *Eimeria frenatus* n.sp. and *Eimeria rochalimai* (Apicomplexa, Eimeriidae) from *Hemidactylus frenatus* (Sauria, Gekkonidae) in Hawaii, USA. *Transactions of the American Microscopical Society* **113**: 390–394.
- , ———, ———, AND C. T. MCALLISTER. 1991. Description of *Isospora schlegeli* sp. nov. (Apicomplexa, Eimeriidae) from gekkonid lizards in the South Pacific. *Canadian Journal of Zoology* **69**: 3108–3110.