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Patterns of introduction of non-indigenous non-marine snails and slugs in the Hawaiian Islands

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The native snails of the Hawaiian Islands are disappearing. One cause is predation by introduced carnivorous snails. Habitat destruction/modification is also important, facilitating the spread of other non-indigenous snails and slugs. Eighty-one species of snails and slugs are recorded as having been introduced. Thirty-three are established: 12 freshwater, 21 terrestrial. Two or three species arrived before western discovery of the islands (1778). During the nineteenth century about one species per decade, on average, was introduced. The rate rose to about four per decade during the twentieth century, with the exception of an especially large number introduced in the 1950s as putative biocontrol agents against the giant African snail, *Achatina fulica*. The geographical origins of these introductions reflect changing patterns of commerce and travel. Early arrivals were generally Pacific or Pacific rim species. Increasing trade and tourism with the USA, following its annexation of Hawaii, led to an increasing proportion of American species. More general facilitation of travel and commerce later in the twentieth century led to a significant number of European species being introduced. African species dominated the 1950s biological control introductions. The process continues and is just part of the homogenization of the unique faunas of tropical Pacific islands.

Keywords: alien species; extinction; biological control; Mollusca; habitat modification.

Introduction

Increasing attention, but almost certainly not enough, is being paid to the threats posed by non-indigenous (alien, introduced, adventive) species to native and endemic biotas, especially of islands.

The native land snail fauna of the Hawaiian Islands is disappearing rapidly. Once it was extremely diverse (over 750 species) and exhibited extremely high endemism (over 99%) (Cowie *et al*., 1995; Cowie, 1996a). Most of these unique species are now extinct or severely threatened, in most cases confined to high elevation refugia (Hadfield, 1986; Solem, 1990; Hadfield *et al*., 1993). One reason (Hadfield, 1986) for this demise has been the deliberate introduction of carnivorous snails in ill-conceived attempts to control another introduced snail, the giant African snail, *Achatina fulica*. Populations of *A. fulica* have not been reduced by the carnivorous snails (Christensen, 1984; Civeyrel and Simberloff, 1996) but native snail populations have been devastated (Hadfield and Mountain, 1981; Hadfield, 1986; Hadfield and Miller, 1989; Hadfield *et al*., 1993). Introduction, both deliberate and not, of non-indigenous snails and slugs is continuing not only in the Hawaiian Islands (Cowie, 1997a) but throughout the islands of the tropical Pacific (Cowie, 1992, in press a; Hopper and Smith, 1992) and to a greater or lesser extent

throughout the world (e.g. Griffiths *et al*., 1993; Cowie, in press b). Indigenous species are perishing primarily through predation and habitat modification, and perhaps competition, and being replaced by a relatively small number of mostly synanthropic, disturbance-tolerant species (Kay, 1995). The terrestrial molluscan biota is being homogenized.

Freshwater mollusc faunas are suffering similar fates. On Pacific islands there are generally far fewer freshwater mollusc species than terrestrial species; many of these freshwater species exhibit diadromous life-cycles; levels of endemism are much lower than in the terrestrial faunas (Cowie, 1997b). Nevertheless, these freshwater faunas are threatened, and for the same reasons as the terrestrial faunas. For instance, in the Hawaiian Islands there are now more non-indigenous than indigenous freshwater species (Cowie *et al*., 1995; Cowie, 1997a); and the same carnivorous snail that has been the major scourge of the terrestrial fauna, *Euglandina rosea*, will even go under water in search of its prey (Kinzie, 1992).

This paper uses data of Cowie (1997a) to investigate patterns in the chronology of introductions of non-indigenous land and freshwater snails in the Hawaiian Islands, reasons for their introduction, their geographic origins, and whether they have become established or not.

Methods

For each species, data on date of introduction, whether it has become established or not, and its region of origin have been drawn from the catalogue of non-marine, non-indigenous snails and slugs of the Hawaiian Islands compiled by Cowie (1997a).

Species included

Cowie (1997a) listed all species and infra-specific taxa known to have been released or to have escaped into the wild in the Hawaiian Islands. He excluded species that have been imported but that have not escaped or been released. Some species have in the past been treated as native/endemic, but are probably introduced (e.g. Ancylidae, Thiaridae). Species that are not demonstrably native or introduced have been termed 'cryptogenic' by Carlton (1996), but all are included here as introduced (although noted as being cryptogenic – see results). The taxonomic status of these listed species was given by Cowie (1997a) following the latest published systematic work on the group. In many cases these systematic works are not recent and modern revision would probably change the status of a number of species. Other species have not been treated systematically since their original description. Except for a small number of cases, the taxonomic status in this paper is as presented by Cowie (1997a). In a few cases, however, among the malacological community there is a consensus that, for instance, two currently separate taxa are in reality synonyms but they have never been formally synonymized; personal experience of the taxa in question might also indicate this to be the case. In these instances, data for the two or more nominal taxa have been combined (e.g. *Cecilioides aperta* and *C. baldwini*), although no formal taxonomic changes are here proposed. In other cases, the taxonomy is so confused that, although a number of species should probably be synonymized, without formal taxonomic revision this is not possible and data for the various species listed by Cowie (1997a) are kept separate (e.g. Thiaridae), thereby overestimating the real number of introduced species. No doubt, however, the list of species is incomplete; other species may have been introduced but perished subsequently, and others may still be present but

have not been recorded or collected. Rather little general collecting has been undertaken, especially in the last few decades, and probably to a much lesser extent on islands other than Oahu, which is the main centre of human population and on which Honolulu is located (as for the native snails; Cowie, 1996a). Most of the collectors, both professional and amateur, have tended to focus on native species and the native habitats in which they occur, and have taken much less interest in the introduced species. The extent of this problem is unknown. Also, identifications in some cases are extremely uncertain (e.g. Physidae, Subulinidae). Despite these inadequacies, the list of Cowie (1997a) is the most comprehensive available and is used here as the best approximation. One species listed by Cowie (1997a) has been excluded from the present considerations (the slug *Limax sandwichiensis*); it was poorly described and never subsequently identified, and probably simply refers to one of the other listed species.

Date of introduction

In most cases this is the date of the first published record or of the earliest dated collections in the Bishop Museum (Honolulu). In some instances, however, there is evidence (e.g. archaeological) that the species was present earlier than the date of the first published record, or the published records give an earlier date as the date on which material was first collected. The earlier date is used here. There is in general an inevitable lag between the actual date of introduction and the date a species was first recorded, either because it took some time before the species was noticed or because, even though it was known to be present, it was simply not collected or recorded in print. Hence, the dates used here are in almost all cases later than the true (but unknown) actual dates of introduction. Accurate dates are, however, known for some species, notably those introduced for biological control in the 1950s.

Whether established or not

The definition of 'established' is inevitably somewhat arbitrary and subjective. For species that are well known, have been in the Hawaiian Islands for a long time, and are still present, it is probably appropriate to classify them as established. But how long a species has to have been present to qualify as established is impossible to define. For a species only very recently introduced, say only a year or two ago, it is probably appropriate not to consider it definitively established even though its population(s) may appear to be thriving. Equally, it is often difficult to determine whether a species has definitively failed to become established; adequate survey work simply has not been done in most cases. In other cases, however, in which a new introduction was monitored, albeit not thoroughly in most cases (e.g. the various species introduced as biological control agents in the 1950s), it may be possible to say with some certainty that the species did not become established. For the present purposes, only those species listed as established or not established by Cowie (1997a) are so considered here. Other species listed by Cowie (1997a) as questionably established, questionably not established, or of unknown status, are treated here as of unknown status.

Region of origin

In most cases this is straightforward. For a small number of species it is known that they have been introduced to the Hawaiian Islands via an intermediate region that is not part of their native range (e.g. *Achatina fulica*: Schalie, 1969; *Pomacea* spp.: Cowie, 1995). Origin is

here treated as this native range, not the intermediate region. However, in some cases there is disagreement in the literature, with origins as different as Africa and India being given by different authors for a particular species. In other cases it is impossible to know the region of origin because the species has been dispersed so widely by human activities, and its taxonomy and phylogeny are poorly understood so that it cannot be associated biogeographically with its nearest relatives. Origin of these species is simply considered unknown.

Results

Cowie (1997a) listed 63 terrestrial and 22 freshwater snail and slug species that have been recorded as aliens in the wild in the Hawaiian Islands. Taking account of the small number of probable synonymies that seem generally acceptable (see above), this reduces to 59 and 22, respectively (Table 1). Of these, perhaps 13 could arguably be considered 'cryptogenic' (Carlton, 1996); this is indicated in Table 1.

The chronology of these introductions is presented in Fig. 1, with cumulative numbers of species introduced and becoming established illustrated in Fig. 2. In terms of the overall pattern, land and freshwater species combined, a very small number of species (three) is known to have arrived prior to western discovery of the islands. The first non-indigenous species, other than these, were not recorded until the 1840s. Following this, up until the end of the 1880s, there was a steady trickle averaging two species per decade, although of the 13 species introduced up to 1889 (six terrestrial and seven freshwater) only five became established (four terrestrial and one freshwater). Then in the 1890s and 1900s the number of new records jumped to ten and eight species per decade respectively, with 16 of the 31 species by then introduced becoming established. This rapid increase in rate of new records then dropped back to about four species per decade for the remainder of the twentieth century (up to 1996) with the exception of a major peak in the 1950s and 1960s, during which two decades 25 species were introduced.

While early introductions were more or less equally divided between terrestrial and freshwater species (six and seven, respectively), after 1890 the balance shifted and a far greater proportion of terrestrial species have been introduced (53 terrestrial, 15 freshwater). Overall, of the 22 freshwater species introduced, 11 have become established (status of the others is unknown), while of the 59 terrestrial species introduced, 22 have become established, 16 have failed, and the status of the remainder is unknown.

Table 2 summarizes the geographic origins of the species, according to the period during which they arrived. The first period (pre-1778) is the period prior to western discovery of the islands; the second (1778–1909) is the period dominated by taxonomic description of introduced species, often without realizing they were not native; the third (1910–1996) is the period during which many species were introduced deliberately or at least were immediately acknowledged as non-indigenous (see Discussion), and only one species is based on an original description (of a subspecies that should probably be synonymized).

Pre-1778 introductions include a Pacific island species (*Lamellidea oblonga*), a species of unknown but certainly adventive origin (*Allopeas gracile*), and a species of unknown origin that may in fact be indigenous (tentatively referred to as *Tryonia protea*). Asian and Australasian species dominate the 1778–1909 period although New World species and a few European and African species did appear. Later introductions are dominated by species from the New World (North, South and Central America, and the Caribbean), an

Table 1. Introduced snail and slug species in the Hawaiian Islands, with date of first record or introduction, whether established or not, and geographical origin

Species	Date	Whether established	Region of origin	Remarks
Freshwater species				
Ampullariidae				
Pila conica	1966	established	Asia	Introduced for food
Pomacea bridgesii	1962	established	S. America	Probably introduced via the aquarium trade from the USA
Pomacea canaliculata	1989	established	S. America	Probably introduced for food from SE Asia
Pomacea paludosa	1969	unknown	N. America	Probably introduced via the aquarium trade
Ancylidae				
*Ferrissia sharpi**	1900	established	unknown	May be indigenous
Bithyniidae				
Bithynia robusta minor	1940	unknown	China	Not known if deliberate or accidental introduction
Hydrobiidae				
*Tryonia protea**	pre-1778	unknown	N. America	Only tentatively identified. May be indigenous
[Genus] *porrecta**	1845	unknown	unknown	May not be distinct from *T. protea*. Correct genus unknown
Lymnaeidae				
Fossaria viridis	1890	established	Asia	Not known if deliberate or accidental introduction
Pseudosuccinea columella	1950	established	N. America	Not known if deliberate or accidental introduction
Physidae				
*Physa compacta**	1870	unknown	unknown	Taxonomic status and status as introduced or not very unclear
Physa elliptica	1969	unknown	N. America	Not known if deliberate or accidental introduction
Physa virgata	1994	established	N. America	Probably present much earlier than when first recorded
Planorbidae				
Planorbella duryi	1969	established	N. America	Includes records of ssp. *normale*. Probably an aquarium trade introduction
Thiaridae				
*Melanoides tuberculata**	1994	established	unknown	No doubt present long before the first record, perhaps prehistorically
*Tarebia granifera**	1856	established	unknown	Possibly introduced prehistorically
*Tarebia lateritia**	1954	unknown	unknown	Possibly a synonym of *granifera*
*Thiara baldwini**	1899	unknown	unknown	Possibly a synonym of other thiarid species
*Thiara indefinita**	1856	unknown	unknown	Possibly a synonym of other thiarid species

Table 1. (*Continued*)

Species	Date	Whether established	Region of origin	Remarks
*Thiara kauaiensis**	1870	unknown	unknown	Possibly a synonym of other thiarid species
*Thiara verrauiana**	1856	unknown	unknown	Possibly a synonym of other thiarid species
Viviparidae				
Cipangopaludina chinensis	1900	established	Asia	Probably introduced for food
Terrestrial species				
Achatinellidae				
*Lamellidea oblonga**	pre-1778	established	Pacific	Possibly an accidental Polynesian introduction
Achatinidae				
Achatina fulica	1936	established	Africa	Originally introduced deliberately from Japan
Arionidae				
Arion sp.	1981	unknown	?Europe, ?N. America	Probably an accidental introduction
Ariophantidae				
Parmarion martensi	1996	unknown	Asia	Only tentatively identified. Probably an accidental introduction
Athoracophoridae				
Athoracophorus sp.	1896	unknown	New Zealand	A very tentative record. Probably an accidental introduction
Bradybaenidae				
Bradybaena similaris	1893	established	Asia	Probably an accidental introduction
Camaenidae				
Papuina barnaclei	1877	not established	Admiralty Islands	Probably recorded in Hawaii based on mislabelled specimens
Cerionidae				
Cerion casablancae	1922	not established	Bahamas	Deliberate introduction
Cerion viaregis	1922	not established	Bahamas	Deliberate introduction
Cerion sp.	1922	not established	Cuba	Deliberate introduction
Clausiliidae				
[Genus] sp.	1965	not established	unknown	Not identified to genus or species. Probably an accidental introduction
Ferussaciidae				
Cecilioides aperta	1892	unknown	West Indies	Includes records of the probable synonym *baldwini*. Probably accidental

Table 1. (*Continued*)

Species	Date	Whether established	Region of origin	Remarks
Helicarionidae				
[Genus] sp.	1994	unknown	unknown	Probably an accidental introduction
Helicidae				
Helix aspersa	1952	established	Europe	Probably an accidental introduction, but possibly introduced for food
Helminthoglyptidae				
Monadenia fidelis	1923	not established	N. America	Accidental introduction
Limacidae				
Deroceras laeve	1896	established	Holarctic	Includes records of the probable synonyms *globosum* and *perkinsi*
Deroceras reticulatum	1963	unknown	Europe	Probably an accidental introduction
Limax flavus	1948	unknown	Europe	Probably an accidental introduction
Limax maximus	1931	established	Europe	Probably an accidental introduction
Limax tenellus	1896	unknown	Europe	Probably an accidental introduction
Limax valentianus	1982	unknown	Europe	Probably an accidental introduction
Milacidae				
Milax gagates	1897	established	Europe	Probably an accidental introduction
Oleacinidae				
Oleacina oleacea	1956	not established	West Indies	Biological control of *Achatina fulica*
Oleacina sp.	1956	not established	Cuba	Biological control of *Achatina fulica*
Salasiella sp.	1956	not established	Cuba	Biological control of *Achatina fulica*
Philomycidae				
Meghimatium striatum	1846	established	Asia	Probably an accidental introduction
Polygyridae				
Polygyra cereolus	1995	unknown	N. America	Probably an accidental introduction
Pupillidae				
Gastrocopta pediculus	1862	unknown	? Asia	Includes records of the probable synonym *nacca*. Probably accidental
Gastrocopta servilis	1892	established	Neotropics	Includes records of the probable synonym *kailuana*. Probably accidental.
Pupisoma orcula	1912	unknown	Asia	Probably an accidental introduction

Table 1. (*Continued*)

Species	Date	Whether established	Region of origin	Remarks
Rhytididae				
Natalina cafra	1959	not established	Africa	Only very tentatively identified. Biological control of *A. fulica*
Spiraxidae				
Euglandina rosea	1955	established	N. America	Biological control of *Achatina fulica*
Streptaxidae				
Edentulina affinis	1957	not established	Africa	Biological control of *Achatina fulica*
Edentulina obesa bulimiformis	1957	not established	Africa	Biological control of *Achatina fulica*
Gonaxis kibweziensis	1952	established	Africa	Biological control of *Achatina fulica*
Gonaxis quadrilateralis	1957	established	Africa	Biological control of *Achatina fulica*
Gonaxis vulcani	1956	not established	Africa	Biological control of *Achatina fulica*
Gulella bicolor	1940	not established	unknown	Biological control of *Achatina fulica* and *Subulina octona*
Gulella wahlbergi	1956	unknown	Africa	Biological control of *Achatina fulica*
Ptychotrema walikalense	1956	unknown	Africa	Biological control of *Achatina fulica*
Ptychotrema sp.	1956	unknown	Africa	Biological control of *Achatina fulica*
Streptaxis contundata	1961	not established	S. America	Biological control of *Achatina fulica*
Strobilopsidae				
Strobilops aenea	1944	unknown	N. America	Probably an accidental introduction
Subulinidae				
Allopeas clavulinum	1900	established	Africa	Includes records of the probable synonym *hawaiiense*
Allopeas gracile	pre-1778	established	unknown (? Neotropics)	Possibly an accidental Polynesian introduction
Opeas beckianum	1914	unknown	C. and S. America	Probably an accidental introduction
Opeas hannense	1906	unknown	Tropical C. America	Probably an accidental introduction
Opeas mauritianum	1906	unknown	unknown	Includes records of the probable synonym *prestoni*. Probably accidental
Opeas opella	1906	established	Asia	Probably an accidental introduction

Table 1. (*Continued*)

Species	Date	Whether established	Region of origin	Remarks
Paropeas achatinaceum	1904	unknown	Asia, Australasia	Probably an accidental introduction
Subulina octona	1903	established	Neotropics	Probably an accidental introduction
Veronicellidae				
Laevicaulis alte	1900	established	Africa	Probably an accidental introduction
Vaginula plebeia	1978	established	Neotropics	Probably an accidental introduction
Veronicella cubensis	1985	unknown	Cuba	Probably an accidental introduction
Zonitidae				
Hawaiia minuscula	1850	established	N. America	Probably an accidental introduction
Oxychilus alliarius	1937	established	Europe	Probably an accidental introduction
Oxychilus cellarius	1963	unknown	Europe	Probably an accidental introduction
Striatura sp.*	1937	established	unknown	May be indigenous
Zonitoides arboreus	1928	established	N. America, West Indies	Probably an accidental introduction

Data are from Cowie (1997a), which should be consulted for additional details and explanations regarding individual species. Note that identifications are frequently highly tentative.

* Species that arguably could be considered 'cryptogenic' (Carlton, 1996).

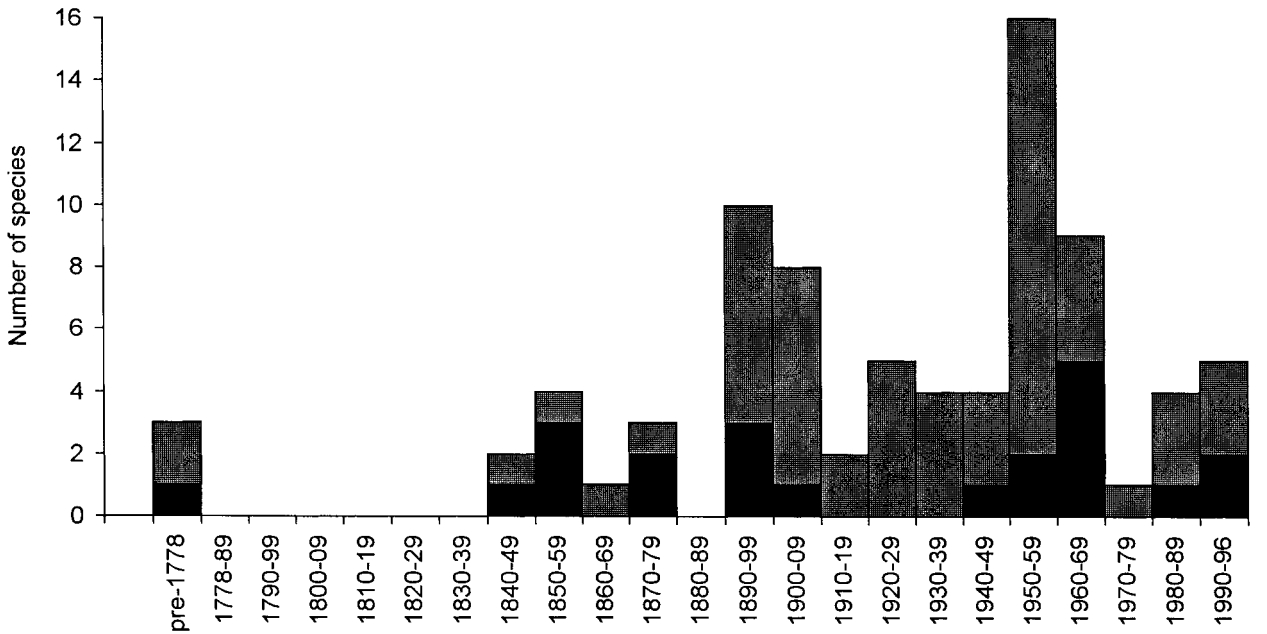

Figure 1. Numbers of non-indigenous land (hatched) and freshwater (black) species of snails and slugs newly recorded in the Hawaiian Islands, by decade up to the end of 1996.

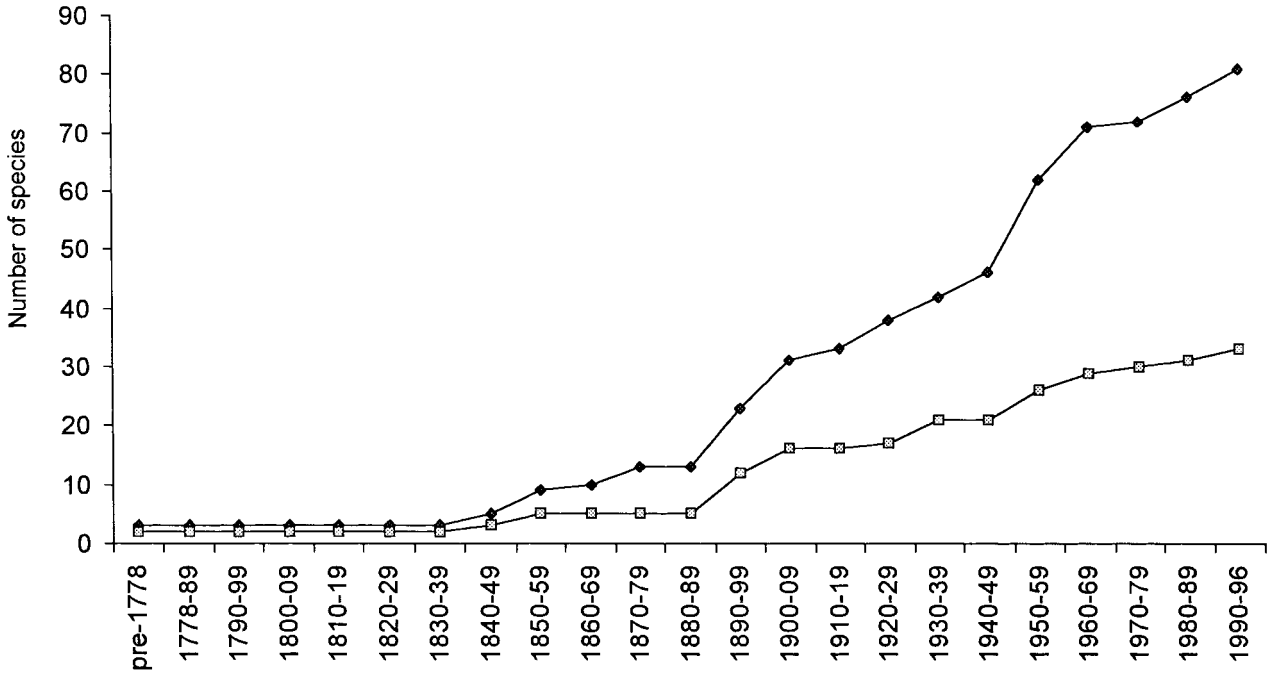

Figure 2. Cumulative numbers of land and freshwater species of snails and slugs recorded as introduced to the wild (upper line) and established in the wild (lower line) in the Hawaiian Islands, by decade.

Table 2. Region of origin of the introduced snails and slugs in the Hawaiian islands, summarized by the period during which they arrived

Region of origin	pre-1778	1778–1909	1910–1996	Total
Pacific	1	–	–	1
Asia/Australasia	–	9	4	13
New World	–	6	22	28
Europe	–	3	8	11
Africa	–	2	10	12
Unknown	2	8	6	16
Total	3	28	50	81

increased number of European and African species, and a continuing arrival of species from the west (Asia and Australasia). The differences between the 1778–1909 and 1910–1996 periods in the predominant regions of origin of the introduced species are significant (log-likelihood G test on the data in Table 2, excluding the pre-1778 period and excluding species of unknown origin and the single Pacific species; $G = 10.66$, $p < 0.025$, 3 d.f.). One species (*Deroceras laeve*) is Holarctic and one (*Arion* sp.) is of European or North American origin, but both are included among the European species in Table 2; placing them with the New World species reduces the overall significance only marginally.

Discussion

The three species arriving in the islands prior to 1778 could be natural colonizations, although they have generally been presumed to have been carried by Polynesian voyagers. They have been recorded in archaeological deposits that have been dated to before 1778 (Christensen and Kirch, 1986; Athens and Ward, 1993; Athens *et al*., 1994); or have been inferred as having arrived pre-1778 on the basis of their distribution elsewhere in the Pacific (Cooke and Kondo, 1960; Christensen and Kirch, 1981). There are conflicting views on the date of arrival of the first humans in the Hawaiian Islands: as early as the first century AD (Hunt and Holsen, 1991); around AD 300 or 400 (Kirch, 1985); or perhaps even as late as AD 500 to 700 (Athens *et al*., 1992). Whatever the true date, Polynesians had been visiting the islands for at least a thousand years before westerners first arrived. That only two or three non-indigenous species of snails became established over this period is remarkable, especially given the immense diversity in the Pacific of very small species that could easily be inadvertently transported (Cowie, 1997b). Although there is no adequate compilation of Pacific island land snail diversity, New Guinea is probably home to about 1000 species, New Caledonia perhaps 400, Vanuatu has at least 130, the tiny island of Rapa has about 100, the Society Islands probably around 200 (Cowie, 1997b). Given the extremely high levels of endemism among Pacific island land snails, an estimate of around 5000 species seems not unreasonable, although essentially a guess. Nevertheless, the pool from which Polynesian voyagers could have brought snails to the Hawaiian Islands might yet have been much smaller than this. The Marquesas, the islands from which the first Hawaiian colonizers are generally thought to have originated (Kirch, 1985), harbour only 53 species (Garret, 1887), although this is no doubt an underestimate. These snails (or their eggs) were most likely carried accidentally in soil associated with crop plants carried to

their new homes by the Pacific islanders. The prehistoric non-indigenous Hawaiian snail fauna appears to be a severely attenuated subset of the non-indigenous prehistoric fauna of the south-west Pacific (Christensen and Kirch, 1981).

It was only in the middle of the nineteenth century that naturalists really began to take note of the Hawaiian biota, describing many new, supposedly endemic species (Kay, 1972). Six of the ten introduced species first recorded between 1840 and 1889 were originally described from the Hawaiian Islands. The first records of three of the other four are based on the original description of a junior synonym, and of the fourth on the original description of a very dubious subspecies. The concept of species being introduced artificially was poorly developed, and all these records are simply a product of this period's increasingly active description of new species. No doubt some of them were introduced earlier than this, during the period 1778–1839, so that, arguably, these ten species trickled in over a period of more than a century (1778–1889), less than one species per decade. No doubt other species were introduced but failed before they were recorded. Some of these may have survived following reintroductions. It is only much more recently that we have any knowledge of failed introductions (for instance, the documented introductions of many species brought in as putative biological control agents against *Achatina fulica*). In general, lack of records of failed introductions cause huge problems in studies of this kind (Moulton and Pimm, 1986; Simberloff, 1986, 1995). Most of the species introduced during this early period were undoubtedly introduced inadvertently, probably mostly associated with agricultural and other plant products. Solid ballast, now no longer used, may also have been involved (US Congress, Office of Technology Assessment, 1993).

The peak of introductions between 1890 and 1909 (Fig. 1) is in large part simply an artifact of the culmination of this increasing taxonomic and later monographic revisionary activity. Half of the 18 new records in these two decades are based on original descriptions (three species), original descriptions of junior synonyms (three species), probable junior synonyms (one species) and dubious subspecies (two species). Many of these species, in fact, could well have arrived decades earlier and have simply not been recorded. However, the rate of faunal introductions in general greatly increased from about 1870 to 1910 as plantation agriculture, notably sugar, was developing rapidly (Cuddihy and Stone, 1990), and foreign influence was growing. There was no quarantine. This 1890–1910 peak may indeed represent, at least in part, a real surge of accidental introductions associated with the introduction of an array of new crop plants and varieties. Reflecting this more generally, an enormous number of putative biological control agents were introduced during this period to combat insect pests that had arrived accidentally, associated with this agricultural development (Swezey, 1931).

The reduced number of new introductions following this 1890–1909 peak represents the decline in description of new species, as the majority had by then been dealt with, and the realization of the introduced status of species that previously might have been described as new simply because they were undescribed in the Hawaiian fauna. Quarantines were also beginning to be established by about 1910. Nevertheless, the introduction of about four species per decade contrasts with the much lower rate (arguably less than one per decade) for most of the nineteenth century. This rate of four or so per decade continues to the present, with new species continuing to be found: *Polygyra cereolus* in 1995 (Cowie, 1996b) and the provisionally identified *Parmarion martensi* in 1996 (Cowie, 1997a). The advent of regular air travel to the Hawaiian Islands since the 1930s, perhaps combined with increased military activities during the Second World War and the Korean and Vietnam

Wars, has probably facilitated this increased rate of introductions (Beardsley, 1979; US Congress, Office of Technology Assessment, 1993). Snails and slugs have been brought in both deliberately and unintentionally, legally and illegally, for numerous purposes. Many have probably been introduced inadvertently along with potted plants associated with Hawaii's large and powerful horticultural industry. Possibly, others have been introduced inadvertently attached to inadequately inspected military and other equipment, in cargo containers, and any number of other possibilities. Others have been brought in by the aquarium trade (e.g. *Pomacea bridgesii, Planorbella duryi*), by private individuals as food items (*Pomacea canaliculata*) or as ornamentals (*Achatina fulica*), and as biological control agents (see below). The pathways via which non-indigenous species (not just snails) arrive are various, but include hand carriage on aircraft, the mail service, private boats, commercial shipping, and so on (US Congress, Office of Technology Assessment, 1993). This relatively constant stream of introductions during the twentieth century contrasts remarkably with the changing rate of introductions of birds (Moulton and Pimm, 1983; Simberloff and Boecklen, 1991). Following gradual introductions of birds up to the 1920s, there was a sudden influx around 1930, followed by a distinct lull up to 1959, and something of a resurgence between 1960 and 1980. The explanation is that most birds have been brought to the islands deliberately, in contrast to the snails and slugs (at least those not brought in for biological control – see below). For instance, in 1930 a society was formed, the Hui Manu, with the express purpose of bringing in and releasing large numbers of birds, which it did (Dillingham, 1936; Simberloff and Boecklen, 1991).

A major perturbation of this relatively constant stream of introductions of snails and slugs occurred in the 1950s and to a lesser extent the 1960s because of the deliberate introduction of a large number of carnivorous land snail species as potential biological control agents against the giant African snail, *Achatina fulica,* previously introduced in the 1930s (Krauss, 1964). Of the18 land snail species introduced in the 1950s and 1960s (15 of them as putative control agents for *Achatina fulica*), luckily nine did not become established. The status of five others is unknown, but they are certainly not common and probably are not causing significant problems. However, four became established, three of them carnivorous species introduced to control *A. fulica*: *Euglandina rosea*, *Gonaxis kibweziensis* and *G. quadrilateralis*. The two *Gonaxis* spp. may have impacted native snail faunas; *E. rosea* has devastated them, and continues to do so. None has impacted *A. fulica*, which has declined for other, unknown reasons (discussed briefly by Cowie, 1992).

The fact that *Achatina fulica* is declining illustrates the fact that introduction and establishment of non-indigenous species is a dynamic process. Species such as *A. fulica*, generally and reasonably thought of as established, may yet decline to a point where they are vulnerable to local extinction. The veronicellid slug *Laevicaulis alte*, first recorded in the Hawaiian Islands at the turn of the century, became widespread and abundant, but is now relatively rarely seen. Anecdotal observations suggest that its decline has coincided with the introduction in the 1970s of another veronicellid, *Vaginula plebeia*, which is now far more common. Competition between them could explain this change, as at first glance they appear similar ecologically, although what they might actually be competing for is unknown.

The native land snail fauna of the Hawaiian Islands has been derived almost exclusively via *in situ* evolutionary radiation from a small number of original colonizers (Cowie, 1996a, 1997b). The extreme isolation of the islands meant that an equilibrium between immigration and extinction, determining the number of species that could coexist in the

islands and dependent on island area – the classic MacArthur and Wilson (1967) theory of island biogeography – played an almost negligible part in structuring the land snail communities of the islands. Now, however, the islands are not so isolated. Non-indigenous species arrive on airplanes and ships. A dynamic equilibrium may well become established, just as has been argued for introduced birds in the Hawaiian Islands, with losses even of species that have survived for decades (Moulton and Pimm, 1983). The native species may participate in this process. They already do inasmuch as *Euglandina rosea* at least has had major impacts on them, but competition between native and non-native snails has not been investigated. In fact, competitive interactions both between native and non-native species and among non-native species may not be important (Simberloff and Boecklen, 1991). Non-native species may simply be taking advantage of opportunities never before exploited by a 'disharmonic' native fauna, or opportunities newly created by gross, human-mediated habitat modification, occupying areas from which native species have long since disappeared (Simberloff, 1995). The native species, both snails (e.g. Hadfield, 1986; Solem, 1990; Hadfield *et al*., 1993) and other elements of the fauna, have already mostly become confined to high elevation native forest; while the non-native species are generally, although with exceptions, found in disturbed low and mid-elevation habitats. And if certain species have an intrinsically greater colonization ability (Simberloff and Boecklen, 1991) then these species will become permanently established and not participate in an ever-changing equilibrium involving species of lesser colonizing ability. Such turnover may occur but may be relatively trivial (Williamson, 1989). Certainly, the number of established non-indigenous species of snails and slugs in Hawaii continues to rise. As yet, there is no hint of a levelling off or an approach to an equilibrium (Fig. 2). The amount of effort expended in attempting to introduce a particular species may also have an effect on its likelihood of survival (Duncan, 1997), but the significance of this for snails cannot be assessed except perhaps for the determined efforts to establish carnivorous species for the control of *Achatina fulica* (at least 3 established out of 15 introduced, see above).

The dynamics of establishment and spread of introduced snails through the archipelago are essentially unknown. Much of the earlier literature simply records presence in the archipelago, without specifying a particular island. Subsequent records on individual islands may therefore not accurately reflect spread from island to island. Thus the kind of analyses undertaken by Moulton and Pimm (1983) and Simberloff and Boecklen (1991) for the introduced birds is not possible. Equally, spread within islands is impossible to document; there has simply not been enough field survey work. Many introductions are characterized by a lag phase during which numbers of the introduced species remain low (Baskin, 1996; Crooks and Soulé, 1996). Subsequent rapid expansion is triggered by one of many factors (Crooks and Soulé, 1996). But then after a period of high numbers, populations decline. In general, the data are not available to assess these kinds of temporal patterns of invasion for the introduced snails and slugs, except to say that some species at least appear to have exhibited very short lag times (e.g. *Euglandina rosea*: Kay, 1995; *Pomacea canaliculata*: Cowie, in press b), and that others do indeed seem to be declining after reaching extremely high numbers (above).

The significant patterns in the geographic origins of the introduced species over time (Table 2) are in general easily explained. Pre-1778 introductions (only three species) include a Pacific island species (*Lamellidea oblonga*) and a species of unknown origin that was supposed by Solem (1964) to be Neotropical (*Allopeas gracile*). *Allopeas gracile* is now

pan-tropical. Pilsbry (1906–1907) considered it 'probably the most widely distributed land snail in the world'. It may have reached Asia and thence the Pacific well before European discovery of the Hawaiian Islands (Christensen and Kirch, 1981). The third pre-1778 species, also of unknown origin but tentatively identified as the North American *Tryonia protea*, is a freshwater species. Freshwater species seem much less likely than terrestrial species to have been inadvertently transported by Polynesian voyagers. However, this species has been found in sediments that predate European arrival in the Hawaiian Islands (Athens and Ward, 1993; Athens *et al*., 1994), suggesting that it is either native or prehistorically introduced. Both these possibilities are tantalizing because the native snail fauna is almost exclusively associated biogeographically with the rest of the Pacific, Australasia and eastern Asia, not the Americas (Cowie, 1997b). However, it has been tentatively suggested (e.g. Cutter, 1980), that westerners, perhaps Spaniards, had in fact reached the Hawaiian Islands prior to 1778, and the idea that there was contact between early Polynesians and native Americans has from time to time been considered (e.g. Cann and Lum, 1997; R.L. Cann, pers. comm.). Both these intriguing possibilities might explain the presence of this species in the Hawaiian Islands, but resolution of this conundrum requires further research.

During the nineteenth and early twentieth centuries, the majority of species of known origin came from Asia/Australasia and the Americas, that is, the Pacific rim, with only a small number of species from further afield (Europe, Africa). Perhaps the European and African species stood less chance of surviving the long voyage around Cape Horn and into the Pacific, compared to the shorter and less climatically extreme voyages within the Pacific that resulted in the introduction of Asian and American species. Later, as commerce and tourism developed, especially with the USA, which annexed Hawaii in 1898, American species began to predominate more heavily. The increased number of European species tended to arrive in the latter half of the twentieth century (Table 1) as world trade and travel were increasingly facilitated. The large number of African species arriving from 1910 onwards are all deliberate introductions; first *Achatina fulica* (which was introduced from Japan in the 1930s), and then the carnivorous snails brought in to control it in the 1950s. Interestingly, the majority of the species of unknown origin (Table 2) arrived early. This would be expected because the early arrivals would likely have been those species already widely distributed by humans before the extensive survey work of the nineteenth century got under way.

The reasons why certain species are more likely than others to become established have attracted much discussion (e.g. Moulton and Pimm, 1986; Simberloff, 1986; Rejmánek, 1996). These reasons seem to include, notably, 'r-selected' life-history traits, generalist food requirements, efficient dispersal, wide habitat tolerance, and a match of their habitat requirements to the often disturbed situations in which they initially find themselves (see also Kay, 1995). However, the reasons for success or failure of any particular introduction may yet be highly idiosyncratic and not generalizable (Simberloff, 1986). Possibly, the absence of native species with appropriate niches, especially in highly modified habitats, rather than the alien species' inherent invasibility or the inherent vulnerability of the region, may be especially important (Simberloff, 1995; Baskin, 1996; Crooks and Soulé, 1996). Although it is not possible to evaluate rigorously all the non-indigenous snails and slugs in Hawaii from these perspectives (because there is insufficient basic knowledge of most of them), it is clear that a significant number of those species that have established successfully are the same species that have succeeded in many other regions, notably

Achatina fulica, *Bradybaena similaris*, *Vaginula plebeia*, *Euglandina rosea*, and some of the subulinids among the terrestrial species (e.g. in New Caledonia; Gargominy *et al*., 1996), and *Pomacea canaliculata* and the thiarids among the freshwater species (e.g. in South-east Asia; Cowie, in press b). These species certainly seem to possess at least some of the predicted characteristics. Adequate documentation of the alien snail faunas of other island groups is not available to allow this comparison to be taken further, but the story mirrors that of the birds, for which Simberloff and Boecklen (1991) have also argued that the successful colonizers in Hawaii are the same species that are successful colonizers elsewhere (but see Moulton and Sanderson, 1997).

How important has this influx of non-indigenous snails and slugs been in the decline of the native snail fauna? Clearly, predation by *Euglandina rosea* has been of major significance (e.g. Hadfield, 1986; Hadfield *et al*., 1993; Civeyrel and Simberloff, 1996) and other predatory snails (*Gonaxis* spp., in particular) may have had an impact. Also, it is possible that availability of abundant non-indigenous snails has allowed *E. rosea* (and other snail predators like the flatworm *Platydemus manokwari* and the suite of insect species introduced to control the freshwater snail *Fossaria viridis*; references in Cowie, 1997a) to exist in much higher numbers than would otherwise be possible, thereby exacerbating its impact on native snails. Diseases identified in non-indigenous species may have been transferred to native species that were previously free of them (Hadfield, 1986). High frequencies of leucodermic lesions have been recorded in populations of *Achatina fulica* (Mead, 1979); and both *A. fulica* and *E. rosea* act as vectors for the rat lungworm (*Angiostrongylus cantonensis*), which may have deleterious effects on the snails' health, although this has not been demonstrated (Hadfield, 1986). Miller (1993) mentioned a possible disease affecting shells of native achatinelline tree snails in the Hawaiian Islands. But the possible impacts of introduced diseases remain purely speculative. There is no evidence that introduced species have out-competed and displaced native species. The relatively slow ecological change wrought by Polynesians prior to 1778 (Cuddihy and Stone, 1990) certainly led to changes in faunal composition (Christensen and Kirch, 1986); new species (including native species with different ecological requirements) may indeed have overlapped spatiotemporally with the original species present, but whether the changing dynamics of their competitive interactions or simply their relative fit to the changed ecology was the proximate cause of the decline of the original inhabitants is unknown. However, the vast majority of the non-indigenous species arrived after 1778 during times (especially in the twentieth century) when habitat change was progressing at a much faster rate. Native species were probably extirpated rapidly from many areas, leaving these areas vacant; the non-native species appear, at least initially, to have occupied habitats that had already been seriously modified by humans and from which native species had already disappeared, as has been suggested for insects (Beardsley, 1979). Some non-native species (e.g. the slug *Limax maximus*) do, however, seem confined to less disturbed habitats. Whether they interact (or interacted) with native species is unknown, although even in these relatively undisturbed habitats, the absence of native species may yet be due to other causes (e.g. rat predation, predation by *E. rosea*). There is, therefore, little ground for considering the introduced snails and slugs to have had major direct ecological impacts on the native Hawaiian snail fauna, with the overwhelming exception of predation by *Euglandina rosea*.

However, introductions continue and native species continue to decline. Carnivorous snails are still considered elsewhere as potential biological control agents, despite their total destruction of entire endemic faunas (Murray *et al*., 1989). As the native/endemic

species disappear (for whatever reason) they are being replaced by a small number of increasingly widespread disturbance-tolerant synanthropic species that are rapidly coming to dominate the faunas of Pacific islands and other tropical and subtropical regions.

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References

Athens, J.S. and Ward, J.V. (1993) Paleoenvironmental investigations at Hamakua Marsh, Kailua, Oahu, Hawaii. Unpublished report. Honolulu: International Archaeological Research Institute, Inc.

Athens, J.S., Ward, J.V. and Wickler, S. (1992) Late Holocene lowland vegetation, Oahu, Hawaii. *New Zealand J. Archaeol.* **14**, 9–34.

Athens, J.S., Erkelens C., Ward, J.V, Cowie, R.H. and Pietrusewsky, M. (1994) The archaeological investigation of inadvertently discovered human remains at the Piikoi and Kapiolani intersection, Kewalo, Waikiki, Oahu, Hawaii. Unpublished report. Honolulu: International Archaeological Research Institute, Inc.

Baskin, Y. (1996) Curbing undesirable invaders. *BioScience* **46**(10), 732–6.

Beardsley, J.W. (1979) New immigrant insects in Hawaii: 1962 through 1976. *Proc. Hawaii. Ent. Soc.* **13**(1), 35–44.

Cann, R.L. and Lum, J.K. (1997) Mankind and Pacific biogeography. In *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes* (A. Keast and Scott E. Miller, eds) pp. 437–43. Amsterdam: SPB Academic Publishing [printed date 1996].

Carlton, J.T. (1996) Biological invasions and cryptogenic species. *Ecology* **77**(6), 1653–5.

Christensen, C.C. (1984) Are *Euglandina* and *Gonaxis* effective agents for biological control of the Giant African Snail in Hawaii? *Am. Malacol. Bull.* **2**, 98–9.

Christensen, C.C. and Kirch, P.V. (1981) Nonmarine molluscs from archaeological sites on Tikopia, southeastern Solomon Islands. *Pac. Sci.* **35**(1), 75–88.

Christensen, C.C. and Kirch, P.V. (1986) Nonmarine molluscs and ecological change at Barbers point, Oahu, Hawaii. *Bishop Mus. Occas. Pap.* **26**, 52–80.

Civeyrel, L. and Simberloff. D. (1996) A tale of two snails: is the cure worse than the disease? *Biodivers. Conserv.* **5**, 1231–52.

Cooke, C.M., Jr and Kondo, Y. (1960) Revision of Tornatellinidae and Achatinellidae (Gastropoda, Pulmonata). *Bishop Mus. Bull.* **221**, 1–303.

Cowie, R.H. (1992) Evolution and extinction of Partulidae, endemic Pacific island land snails. *Phil. Trans. R. Soc. Lond.* B **335**, 167–91.

Cowie, R.H. (1995) Identity, distribution and impacts of introduced Ampullariidae and Viviparidae in the Hawaiian Islands. *J. Med. Appl. Malacol.* **5**[1993], 61–7.

Cowie, R.H. (1996a) Variation in species diversity and shell shape in Hawaiian land snails: in situ speciation and ecological relationship and ecological relationships. *Evolution* **49**(6)[1995], 1191–1202.

Cowie, R.H. (1996b) New records of introduced land and freshwater snails in the Hawaiian Islands. *Bishop Mus. Occas. Pap.* **46**, 25–7.

Cowie, R.H. (1997a) Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. *Bishop Mus. Occas. Pap.* **50**, 1–66.

Cowie, R.H. (1997b) Pacific island land snails: relationships, origins, and determinants of diversity. In *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes* (A. Keast and Scott E. Miller, eds) pp. 347–72. Amsterdam: SPB Academic Publishing [printed date 1996].

Cowie, R.H. (in press a) Catalog of the nonmarine snails of Samoa. *Bishop Museum Bull. Zool.*

Cowie, R.H. (in press b) Apple snails as agricultural pests: their biology, impacts, and management. In *Molluscs as Crop Pests* (G.M. Barker, ed.). London: CABI.

Cowie, R.H., Evenhuis, N.L. and Christensen, C.C. (1995) *Catalog of the Native Land and Freshwater Molluscs of the Hawaiian Islands*. Leiden: Backhuys Publishers.

Crooks, J. and Soulé, M.E. (1996) Lag times in population explosions of invasive species: causes and implications. In *Proceedings of the Norway/UN Conference on Alien Species. Trondheim, 1–5 July 1996* (O.T. Sandlund, P.J. Schei and A. Viken, eds) pp. 39–46. Trondheim: Directorate for Nature Management and Norwegian Institute for Nature Research.

Cuddihy, L.W. and Stone, C.P. (1990) *Alteration of Native Hawaiian Vegetation. Effects of Humans, their Activities and Introductions*. Honolulu: University of Hawaii Cooperative National Park Resources Studies Unit.

Cutter, D. (1980) The Spanish in Hawaii: Gaytan to Marin. *Hawaii. J. Hist.* **14**, 16–25.

Dillingham, W.F. (1936) Hui Manu – friend of birds. *Paradise of the Pacific* **48**(12), 20–1.

Duncan, R.P. (1997) The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *Am. Nat.* **149**(5), 903–15.

Gargominy, O., Bouchet, P., Pascal, M., Jaffré, T. and Tourneur, J.-C. (1996) Conséquences des introductions d'espèces animales et végétales sur la biodiversité en Nouvelle Calédonie. *Rev. Ecol.* (*Terre Vie*) **51**, 375–402.

Garrett, A. (1887) Mollusques terrestres des Iles Marquises (Polynésie). *Bull. Soc. Malacol. Fr.* **4**, 1–48.

Griffiths, O., Cook, A. and Wells, S.M. (1993) The diet of the introduced carnivorous snail *Euglandina rosea* in Mauritius and its implications for threatened island gastropod faunas. *J. Zool.* **229**, 79–89.

Hadfield, M.G. (1986) Extinction in Hawaiian achatinelline snails. *Malacologia* **27**(1), 67–81.

Hadfield, M.G. and Mountain, B.S. (1981) A field study of a vanishing species, *Achatinella mustelina* (Gastropoda, Pulmonata), in the Waianae Mountains of Oahu. *Pac. Sci.* **34**(4)[1980], 345–58.

Hadfield, M.G. and Miller, S.E. (1989) Demographic studies on Hawaii's endangered tree snails: *Partulina proxima*. *Pac. Sci.* **43**(1), 1–16.

Hadfield, M.G., Miller, S.E. and Carwile, A.H. (1993) The decimation of endemic Hawaiian tree snails by alien predators. *Am. Zool.* **33**, 610–22.

Hopper, D.R. and Smith, B.D. (1992) Status of tree snails (Gastropoda: Partulidae) on Guam, with a resurvey of sites studied by H.E. Crampton in 1920. *Pac. Sci.* **46**(1), 77–85.

Hunt, T.L. and Holsen, R.M. (1991) An early radiocarbon chronology for the Hawaiian Islands: a preliminary analysis. *Asian Perspectives* **20**(2), 246–80.

Kay, E.A. (1972) Hawaiian natural history: 1778–1900. In *A Natural History of the Hawaiian Islands. Selected Readings* (E.A. Kay, ed.) pp. 604–53. Honolulu: University of Hawaii Press.

Kay, E.A. (1995) Which molluscs for extinction? In *The Conservation Biology of Molluscs* (E.A. Kay, ed.) pp. 1–7. Gland: IUCN.

Kinzie, R.A., III (1992) Predation by the introduced carnivorous snail *Euglandina rosea* (Ferussac) on endemic aquatic lymnaeid snails in Hawaii. *Biol. Conserv.* **60**, 149–55.

Kirch, P.V. (1985) *Feathered Gods and Fishhooks: an Introduction to Hawaiian Archaeology and Prehistory*. Honolulu: University of Hawaii Press.

Krauss, N.L.H. (1964) Investigations on biological control of Giant African (*Achatina fulica*) and other land snails. *Nautilus* **78**(1), 21–7.

MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton: Princeton University Press.

Mead, A.R. (1979) *Pulmonates. Volume 2B. Economic Malacology with Particular Reference to Achatina fulica*. London: Academic Press.

Miller, S.E. (1993) Final report on surveys of the arboreal and terrestrial snail fauna of American Samoa. Unpublished report. Honolulu: United States Fish and Wildlife Service.

Moulton, M.P. and Pimm, S.L. (1983) The introduced Hawaiian avifauna: biogeographic evidence for competition. *Am. Nat.* **121**(5), 669–90.

Moulton, M.P. and Pimm, S.L. (1986) Species introductions to Hawaii. In *Ecology of Biological Invasions of North America and Hawaii* (H.A. Mooney and J.A. Drake, eds) pp. 231–49. New York: Springer.

Moulton, M.P. and Sanderson, J.G. (1997) Predicting the fate of passeriform introductions on oceanic islands. *Conserv. Biol.* **11**(2), 552–8.

Murray, J., Murray, E., Johnson, M.S. and Clarke, B. (1989) The extinction of *Partula* on Moorea. *Pac. Sci.* **42**[1988], 150–3.

Pilsbry, H.A. (1906–1907) *Manual of Conchology. Second series: Pulmonata*. Vol. XVIII. Achatinidae: Stenogyrinae and Coeliaxinae. Philadelphia: Academy of Natural Sciences.

Rejmánek, M. (1996) Invasive plant species and invasible ecosystems. In *Proceedings of the Norway/UN Conference on Alien Species. Trondheim, 1–5 July 1996* (O.T. Sandlund, P.J. Schei and A. Viken, eds) pp. 60–8. Trondheim: Directorate for Nature Management and Norwegian Institute for Nature Research.

Schalie, H. van der (1969) Man meddles with nature – Hawaiian style. *The Biologist* **51**(4), 136–46.

Simberloff, D. (1986) Introduced insects: a biogeographic and systematic perspective. In *Ecology of Biological Invasions of North America and Hawaii* (H.A. Mooney and J.A. Drake, eds) pp. 3–26. New York: Springer.

Simberloff, D. (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pac. Sci.* **49**(1), 87–97.

Simberloff, D. and Boecklen, W. (1991) Patterns of extinction in the introduced Hawaiian avifauna: a reexamination of the role of competition. *Am. Nat.* **138**(2), 300–27.

Solem, A. (1964) New records of New Caledonian nonmarine molluscs and an analysis of the introduced molluscs. *Pac. Sci.* **18**(2), 130–7.

Solem, A. (1990) How many Hawaiian land snail species are left? and what we can do for them. *Bishop Mus. Occas. Pap.* **30**, 27–40.

Swezey, O.H. (1931) Records of introductions of beneficial insects into the Hawaiian Islands. In *Handbook of the Insects and other Inverbebrates of Hawaiian Sugar Cane Fields* (F.X. Williams, ed.) pp. 368–89. Honolulu: Hawaiian Sugar Planters' Association.

US Congress, Office of Technology Assessment (1993) *Harmful Non-indigenous Species in the United States*. Washington: US Government.

Williamson, M. (1989) The MacArthur and Wilson theory today: true but trivial. *J. Biogeog.* **16**, 3–4.