The introduction and spread of invasive species around the world has been well documented and there is general agreement around the principles of the invasion process (Sakai et al. 2001). Although it is hard to predict the invasion potential of a given species, the likelihood of successful invasion depends on its body mass, geographic range, generalism, migratory tendency, and the environment it invades (Heger & Trepl 2003; Cassey et al. 2004b). Traits such as rapid maturity and multiple reproductive events per season, further increases the likelihood of the establishment of a self-sustaining population (Crawley 1986; Kolar & Lodge 2001). The probability of establishment is also increased by habitat suitability, particularly if the invasive species occupies a vacant niche (Moles & Gruber 2008). Initial colonisation is dependent on arrival of healthy individuals which have the potential to adapt to the new environmental conditions (Chown et al. 2007; Davidson et al. 2011). In addition, successful colonisation and establishment is related to introduction effort (propagule pressure): the number of individuals at each introduction event (propagule size), the number and spatial distribution of discrete introduction events (propagule number) of viable individuals (Ahlroth et al. 2003; Lockwood et al. 2005), and the genetic diversity of the invasive species (Ahlroth et al. 2003).

Once established the further spread of a species appears related to its dispersal ability and the potential dispersal pathways (Wilson et al. 2009). The dynamics of spread are typically characterised by a period of relatively slow population growth (lag phase), followed by rapid population growth, and finally expansion of invasive range (Memmott et al. 2005; Barney 2006). The length of the lag phase (time between the initial colonisation and rapid population growth), may vary with the speed of adaptation to the new environment (Sakai et al. 2001).

The spread of bird species to novel environments has been reported for numerous species including parrots (Cassey et al. 2004a; Shwartz et al. 2009), Eurasian collared dove (Streptopelia decaocto; Eraud et al. 2007), common myna (Acridotheres tristis; Peacock et al. 2007) and house crow (Corvus splendens; Ryall 2010). The introduction of new species may occur by ‘self-introduction’ in which birds reach a new area by themselves, deliberately release for pest control, hunting or nostalgia, accidental or deliberate release via the pet trade, or accidental transportation.
on international shipping (Peacock et al. 2007). The subsequent spread of these species can be assisted by human-modification of the environment (Dean 2000). In addition, life history traits such as high reproductive capacity, dispersal ability and aggressive competitive behaviour are associated with range expansion in introduced bird species (O’Connor 1986).

The southern subspecies of the Australian masked lapwing, known in New Zealand as the spur-winged plover (*Vanellus miles novaehollandiae*), self-introduced into New Zealand as early as 1886 (Oliver 1974). However, the first breeding pair was not recorded until 1932 (Barlow 1972). The species is currently classed as ‘native’ as its arrival in New Zealand predates the establishment of the Wildlife Act 1953 and it is not regarded as an invasive species. However, over the last 70 years the species has spread progressively up the length of the South Island and across the whole of the North Island of New Zealand. In this paper we describe the spread of this species across New Zealand over the last 70 years and analyse the factors associated with its establishment and spread.

Using a method similar to Peacock et al. (2007) for estimating the distribution of common myna in southern Africa, the spread of the spur-winged plover in New Zealand was assessed from records of the presence or absence of birds on a country-wide grid established for national surveys from 1930 to 2004 (Barlow 1972; Bull et al. 1985; Robertson et al. 2007). These surveys were allocated to the following time blocks: 1930-1949, 1950-1969, 1970-1989 and 1990-2004, and were then used to create a distribution map for the whole country from 1930 to 2004. A logistic regression growth curve was used to model the increase in population spread over this time period across South and North Islands (PSAW...
Over the period 1930 to 2004 the number of grid squares where plovers were recorded increased from 1 to 1191 in the South Island and from 9 to 1313 over the period 1969 to 2004 in the North Island (Fig. 1). The increased occupancy of grid squares over time fit a logistic growth model for South Island, North Island and the country as a whole, respectively ($r = 0.943$, $P = 0.001$; $r = 0.998$, $P < 0.05$; and $r = 0.979$, $P < 0.001$, Figs. 2 A, B & C). The lag phase of establishment was estimated from the date of the first recorded presence to the approximate date when the species moved into an exponential growth phase (Figs. 2 A & B). This was estimated to be ~30 years for South Island and 15-20 years for North Island.

The successful establishment of a new species in a novel environment depends on multiple factors, some of which can result in failure to establish (Jeschke & Strayer 2005). The interval of 46 years between the first possible sighting of the spur-winged plover in New Zealand in 1886 (Oliver 1974) and the first recorded breeding pair in 1932 (Barlow 1972) may be an example of this, with the first birds not surviving and the species only later establishing by a later self-introduction. Subsequently, over the last 70 years, the range of the spur-winged plover has expanded throughout most of New Zealand (Fig. 1). The pattern of this spread is consistent with a stratified dispersal model (Shigesada & Kawasaki 1997), whereby spread of a new species is the combination of short-distance range expansion radiating from the initial establishment location (in this case, the Invercargill area) and long-distance ‘jump’ dispersal events as shown by sightings in the period 1969-1979 in the mid- to northern regions of North Island. The pattern of introduction, establishment and spread across both the South Island from 1930s and North Island from the 1960s is similar to that expected of an invasive species with a lag phase followed by a rapid increase in population expansion (Lockwood et al. 2007; Memmott et al. 2005; Barney 2006; Fig. 2 & 3). This pattern is also similar to that reported by Hone (1978), Holzapfel et al. (2006) and Peacock et al. (2007) for the establishment and spread of the common myna in Australia, Israel and southern Africa, respectively.

The lag phases in an invasive species may be a result of a naturally slow population growth trajectory due to low numbers of individuals, low detection rates at low population size, or allee effects of small populations (Keitt et al. 2001; Lockwood et al. 2007). The rapid spread of the spur-winged plover across New Zealand may have been assisted by the introduction of genetic variation from the arrival of new individuals from Australia. Simberloff (2009) reported that the introduction of genetic

Fig. 2. Number of grid squares occupied by spur-winged plover (*Vanellus miles novaehollandiae*) for South Island (top graph), North Island (middle graph) and South and North Islands combined (bottom graph; 1930-2004) (Source: Barlow 1972; Bull et al. 1985; Robertson et al. 2007).
variation may allow the adaptation of species to a new environment. Spread may also have resulted from the newly established population reaching a critical threshold that overcame the constraints of small population size (Keitt et al. 2001; Lockwood et al. 2007). As with the rapid spread of the house crow (Feare & Mungoo 1990), the high reproductive rate of the spur-winged plover (clutches of 1-4 eggs several times per breeding season) and its aggressive behaviour (Heather & Robertson 2005) may have contributed to its spread in New Zealand.

Introduction effort (propagule pressure = propagule number + propagule size) of new species to a novel environment has been shown to be a strong determinant of invasion success in a range of invasive bird species (Veltman et al. 1996; Ahlroth et al. 2003; Duncan et al. 2003; Cassey et al. 2005; Lockwood et al. 2005; Jeschke & Strayer 2006; Simberloff 2009). A meta-analysis by Veltman et al. (1996) showed that introduction effort, as measured by propagule size, of introduced bird species to New Zealand was a significant factor in colonisation success. Memmott et al. (2005) showed that increasing the number of individuals released at any one time (propagule size) resulted in a decrease in the lag phase of the psyllid (Arytainilla spartiophila) when introduced as a biological control agent. Within the current study, the difference in the length of the lag phase in the South Island compared with North Island may be due to the propagule pressure during each introduction/establishment phase. Due to the relatively large distance between Australia and New Zealand, the initial introduction of the species is likely to have involved small numbers of birds and as such would have required considerable time to reach a population mass to allow exponential population growth. However, a shorter lag phase of the species in North Island may be expected due to the relatively short distance between South and North Island and the likelihood of multiple invasions from South Island, i.e., an increase in the propagule number and size arriving in North Island.

Climate/environmental matching is an important factor in the successful establishment and spread of invasive bird species (Duncan et al. 2003; Eraud et al. 2007; Peacock et al. 2007; Shwartz et al. 2009). As New Zealand is within the same general latitude as southern Australia, the spur-winged plover’s native range, it can be assumed that similar climatic conditions would have assisted the introduction of the species (Duncan et al. 2003). As in Australia, the spur-winged plover in New Zealand inhabits open short grassland, wetland or marshland (Thomas 1969; Marchant & Higgins 1993). It will also use stony or sandy areas on the edges of rivers, riverbeds, beaches and estuaries (Barlow 1972) and has adapted to living in open human-modified habitats such as pasture, sports grounds, parks, golf courses, school playing fields and airfields (Thomas 1969; Maunder et al. 2005). Analysis of a range of vertebrate species determined that human affiliation was one of the principle factors determining invasion success across the 3 stages of introduction, establishment and spread (Jeschke & Strayer 2006), while urban association and land transformation was closely associated with the spread of the invasive common myna (Holzapfel et al. 2006; Peacock et al. 2007) and the house crow (Lim et al., 2003; Nyári et al. 2006). The modification of the New Zealand landscape by the clearing of native forest for agricultural purposes and the development of open grassland areas may have resulted in a novel vacant niche (Dean 2000; Moles & Gruber 2008) which has potentially facilitated the occupation by the spur-winged plover on arrival to and subsequent spread across New Zealand.

The spur-winged plover self-introduced into New Zealand and although classified as ‘native’, its establishment and spread across both South and North Islands exhibits similar patterns to that of other invasive species such as the common myna. Although introduction effort (propagule pressure) has been identified as a factor in the establishment success of invasive species (Cassey et al. 2005), due to the lack of information on the number of birds that arrived in New Zealand and a genetic analysis, it is not possible to determine if introduction effort and genetic variation assisted the spread of this bird. However, the bird’s life history characteristics, its occupation of a human-modified novel and vacant niche, and its adaptability to living in close proximity to humans have most likely contributed to the establishment and rapid spread of the spur-winged plover throughout New Zealand.

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LITERATURE CITED


