

# A case study of species assessment in invasion biology: the Village Weaverbird *Ploceus cucullatus*

D. C. Lahti

Lahti, D. C., 2003. A case study of species assessment in invasion biology: the Village Weaverbird *Ploceus cucullatus*. *Animal Biodiversity and Conservation*, 26.1: 45–55.

## Abstract

*A case study of species assessment in invasion biology: the Village Weaverbird Ploceus cucullatus.*— Application of recent insights gained in invasion biology to particular species may aid in addressing a central problem of the field, that of prediction of the dynamics of future introduction and invasion. The Village Weaverbird (*Ploceus cucullatus*) is concluded to be a potential invader of concern in several regions, especially the Mediterranean, Caribbean, and southeastern United States. This conclusion is supported by the introduction and invasion history of the species, factors concluded in recent reviews and quantitative studies to correlate with introduction success or invasiveness in birds, the species' agricultural pest status in its current range, and a published rating system. A proactive stance is recommended since control efforts have met with little success, but certain characteristics of the Village Weaver may provide opportunities for management.

Key words: Invasive species, Introduction success, Agricultural pests, Birds, Ploceidae, *Ploceus cucullatus*.

## Resumen

*Estudio de un caso de evaluación biológica de una especie invasora: el tejedor Ploceus cucullatus.*— La aplicación a determinadas especies de los últimos resultados obtenidos en el campo de la biología de las invasiones podría ayudarnos a abordar un problema clave: predecir cuál será la dinámica de la futura introducción e invasión de ciertas especies. Se ha llegado a la conclusión de que el tejedor *Ploceus cucullatus* constituye un importante invasor potencial en determinadas áreas geográficas, especialmente en el Mediterráneo, el Caribe y el sudeste de Estados Unidos. Esta conclusión se basa en la historia de la introducción e invasión de determinadas especies, así como en los factores recogidos en distintos análisis y estudios cuantitativos orientados a establecer una correlación entre el éxito de la introducción o invasión de estas aves, la situación de las plagas agrícolas causadas actualmente por esta especie, y un sistema de valoración publicado. Dado que los intentos de control no han resultado muy satisfactorios, se recomienda adoptar una actitud proactiva, si bien cabe la posibilidad de que determinadas características de este tejedor brinden ciertas oportunidades de control.

Palabras clave: Especies invasoras, Éxito de la introducción, Plagas agrícolas, Aves, Ploceidae, *Ploceus cucullatus*.

(Received: 8 II 02; Conditional acceptance: 2 V 02; Final acceptance: 4 XI 02)

David C. Lahti, Museum of Zoology and Dept. of Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor, MI 48109, U.S.A.

## Introduction

For decades ecologists have recognized the importance of invasive species, organisms that expand into a new geographical areas and subsequently spread from their points of entry (ELTON, 1958; WILLIAMSON, 1996). A central theme in the political and scientific response to the invasive species problem has been a call for focused research on prediction of the likelihood of an invasion's occurrence and impact: the "Holy Grail of invasion biology" (ENSERINK, 1999). One way in which research may proceed in this area is to apply knowledge about particular candidate species and sites of potential introduction or spread, to our understanding of typical characteristics of invaders and invasion sites. This paper provides such a case study. The Village Weaver (*Ploceus cucullatus*) is a common passerine bird native to sub-Saharan Africa (BANNERMAN, 1949; MACLEAN, 1993; BARLOW et al., 1997). The Village Weaver builds elaborate, enclosed nests in often dense colonies, and prefers the proximity of human habitation and agriculture (COLLIAS & COLLIAS, 1971; LAHTI et al., 2002). Its ecological generalism and its successful establishment on islands to which it has been introduced, along with the agricultural damage it causes (e.g., ADEGOKE, 1983a; MANIKOWSKI, 1984), indicate it as an important candidate for applying recent work in invasion biology. Moreover, in the last two decades this species has been sighted with increasing frequency in the southern United States and Europe, which are outside of its current breeding range (e.g., HIPPI, 1988; PEZZO & MORELLINI, 1999).

This case study aims to: 1. Assemble what is known about the Village Weaver relevant to invasion biology; 2. Assess the likelihood that this species will be an invader of concern in the future; and 3. Determine whether its biology warrants actions to deal with ecological or agricultural problems.

## Regions of past and possible future naturalization

### History of introductions and sightings

The West African form of the Village Weaver (*P. c. cucullatus*) was introduced to the island of Hispaniola long before 1920, when the first specimens were collected (WETMORE & SWALES, 1931). Most researchers believe that the Village Weaver is among those birds described by the eighteenth century historian Moreau de Saint-Méry as having been imported to Haiti from Senegal as cage birds (WETMORE & SWALES, 1931). One source claims a colony to have been established in that country in 1783 (LONG, 1981), and in fact the species could have existed there before that time. By the 1930's the weaverbird was still mainly known from Haiti, and had only been found in

two locations in western Dominican Republic (WETMORE & SWALES, 1931; BOND, 1936). It remained at low densities on the island, and maintained its restricted distribution, through the middle of the twentieth century. As late as 1962 the Dominican Republic was not considered part of its range by MAYR & GREENWAY (1962). In the early 1960's, however, "a population explosion caused it to become so abundant that it became a serious pest to rice crops" (LONG, 1981). Recently the species has been described as widespread and common in both countries on the island (LEVER, 1987; RAFFAELE et al., 1998), although on no other island in the Greater Antilles. Some indication exists that the Hispaniolan population may be currently undergoing a decline, and some areas that have been known to support large colonies no longer do so (personal observation, IV-VI 01; J. W. Wiley, personal communication, III 01).

In about 1880 the western South African form of the Village Weaver (called there the Spotted-Backed Weaver, *P. c. spilonotus*) was introduced to the Mascarene Island of Réunion. In 1886 it was introduced to nearby Mauritius (CHEKE, 1987; JONES, 1996). These introductions were probably due to escapes from captivity (BARRÉ & BARAU, 1982), and researchers are confident that no reintroductions have followed those events (BERLIOZ, 1946; SIMBERLOFF, 1992). As of 1946 the Réunion population was still restricted to the cultivated plains near the coast, but already had a reputation as an agricultural pest (BERLIOZ, 1946). By 1982 it was considered with the House Sparrow (*Passer domesticus*) to be the worst agricultural pest on the island, and was abundant throughout the island in low elevations. On Mauritius the species spread slowly from its point of initial introduction (CHEKE, 1987) and steadily increased in population size through the 1950s when it began to be considered a pest there as well.

Village Weaver specimens were collected from the Cape Verde Islands off the west coast of Africa in 1924 and a breeding attempt was documented in 1993 (HAZEVOET, 1995). Their origin, and whether their presence there has been continuous or intermittent, is unknown, though they are usually presumed to be introduced (LONG, 1981; LEVER, 1987; CRAMP & PERRINS, 1994). A bird established on São Tomé Island has been claimed to be an introduced Village Weaver (MAYR & GREENWAY, 1962). In fact its origin is unknown, and differences in plumage from the mainland Village Weaver have led many to view it as a distinct species (HALL & MOREAU, 1970; NAUROIS, 1994).

The first record of the Village Weaver nesting on Martinique was in 1980 (PINCHON & BENITO-ESPINAL, 1980). The species was described as well established a few years later (BARRÉ & BENITO-ESPINAL, 1985). Though common, it is still reported to be localized in the same area to which it was introduced, at the northern end of the island (RAFFAELE et al., 1998).

In the past two decades the Village Weaver has been found in the wild for the first time in North and South America, and Europe. A single male was seen and photographed in South Carolina in 1988, apparently the first record from the continental United States (HIPPI, 1988). The closest population to South Carolina is on Hispaniola, 1600 km away, although the bird could also have been an escape. The distance from Hispaniola to Florida is 750 km, although no records exist from that state. Hispaniola is of course close to other Caribbean islands, although the weaver is at most a vagrant in Cuba, Jamaica and Puerto Rico. (Despite the claim in LONG (1981) and LEVER (1987) that it exists on Puerto Rico, there is no support for this in the relevant regional works (e.g., BOND, 1936; RAFFAELE et al., 1998)). Recently the Village Weaver has been seen breeding in Venezuela (R. Restall, personal communication, VII 00). Specimens have been collected from the vicinity of Lake Maracaibo, which is 800km south of the Dominican Republic, or 1,200 km east-southeast of Martinique.

In Europe, the Village Weaver has been sighted at least six times in Italy, three of which involved breeding attempts (males building nests) (PEZZO & MORELLINI, 1999). PEZZO & MORELLINI (1999) suggest that the species may survive in the wild in Siena province, and could eventually become established in Central Italy. A breeding attempt has also been documented in the vicinity of Paris (LE MARÉCHAL, 1985). These individuals survived the winter, which suggests that the species may be able to persist in that region. Other breeding attempts in the wild, some successful, are reported from France and Germany (PEZZO & MORELLINI, 1999). In Portugal breeding colonies have reportedly been established (VOWLES & VOWLES, 1994), although whether they persist is unknown. No sources are known for the birds in any of these localities, but they are often assumed to be escapes. The distance from the northern African range limit to Portugal or Italy is approximately 2,500 km.

In sum, three attempts at introduction are known in this species: Hispaniola, Réunion, and Mauritius. All of these were successful, although the Hispaniolan introduction is likely to have consisted of several events over a long period of time. One further naturalized population (Martinique) is of unknown origin. Establishment in Cape Verde, Venezuela, and Portugal is possible but not yet adequately documented. There are no known failed introductions of the Village Weaver, but escapes may have gone unnoticed. No single pattern of population growth characterizes the species in the several areas to which it has been introduced or spread. In the Mascarene Islands the populations have grown and spread steadily, whereas on Hispaniola the density remained low until a population boom and rapid spread occurred. On Martinique the population has grown but remained localized.

### Commercial bird trade

The cage bird trade is probably responsible for much of the Village Weaver's existence outside of its native range; historical records indicate this method of introduction to the islands of Hispaniola, Mauritius, and Réunion over a century ago (WETMORE & SWALES, 1931; BARRÉ & BARAU, 1982; CHEKE, 1987). Data collected between 1974 and 1981 on annual exports of cage birds from Senegal, 13% of which were Ploceids, indicate France as the top importer. France, Spain, Belgium, Holland, Italy, and West Germany accounted for 75% of Senegal's bird trade during that period. The United States was a rising market, overtaking France in 1980 (BRUGGERS, 1983). However, in the U. S. the Village Weaverbird in particular is said to be "seldom kept in captivity, mainly because of its aggressivity" (HIPPI, 1988), and the captive populations that do exist are subject to legislated standards of confinement (BROSSET, 1985). In France the species has been reported to be common merchandise and susceptible to escape due to lack of restrictions (BROSSET, 1985). Some researchers believe that the Village Weaver's recent establishment on the island of Martinique was due to recent bird trade (BARRÉ & BENITO-ESPINAL, 1985), whereas others see this species as one of several that may have been carried to the West Indies by storms from Africa (NORTON, 1989; WEAVER, 1996).

Given the nature of the Ploceid trade and the history of this species' introductions and sightings, the southern United States, the West Indies to northern South America, and southwestern Europe might be considered the regions of most probable introduction.

### **Factors influencing introduction and invasion success**

The ecology and behavior of the Village Weaver were determined from the literature and from observations of natural populations in its natural and introduced ranges during 1999–2001 (see, e.g., LAHTI & LAHTI, 2002). These characteristics, along with habitat information from regions of most probable introduction, were compared with attributes of species and introduction sites that were found in recent reviews and quantitative studies to correlate with the likelihood of introduction success or invasiveness (table 1). Here "introduction" refers to population establishment, whereas "invasion" refers to spread beyond the local area of introduction (KOLAR & LODGE, 2001b). Both intrinsic and extrinsic factors were considered, in the sense of factors that respectively are or are not species-specific traits of the Village Weaver.

In general the Village Weaver fits the characterization of a successfully introduced and invasive bird as described by recent studies (table 1). Of 14 factors found to correlate with introduc-

Table 1. Factors correlated with introduction success and invasiveness in birds, and relation to the Village Weaverbird *Ploceus cucullatus* (VW). Factors in the first column exhibit a correlation with introduction or invasion success. In the second column, numbers following KL are the numbers of quantitative studies testing each factor (number of studies with a significant result / total number of studies), adapted from KOLAR & LODGE (2001b) and subsequent adjustments (based on SOL, 2001; KOLAR & LODGE, 2001a). These studies may not be independent tests of the hypotheses because four of the eight were of New Zealand birds. Other initials in the second column refer to the following studies: LMA. LOCKWOOD et al. (1993); C. CASE (1996); SMC. SORCI et al. (1998); MMS. McLAIN et al. (1999); BD. BLACKBURN & DUNCAN (2001); STL. SOL et al. (2002). No two studies had significant results opposed to each other; <sup>1</sup> CASE (1996) actually measured number of native extinctions, but considered this a proxy for "degree of human activity and habitat destruction and deterioration...". <sup>2</sup> LOCKWOOD et al. (1993) actually measured morphological overdispersion of introduced relative to native species, which they consider to be an indicator of competition. <sup>3</sup> Both of the two significant studies had mixed results (SOL, 2001). <sup>4</sup> BLACKBURN & DUNCAN (2001) actually measured latitudinal difference and proportion of introductions within the same biogeographic region as the source population, but considered these proxies for "climatic and habitat features". <sup>5</sup> No quantitative study has tested whether successfully established or invasive exotic birds tend to become established or invasive in subsequent introductions as well. The factor is included here because of its plausibility (SIMBERLOFF & BOECKLEN, 1991; VERMEIJ, 1996).

*Tabla 1. Factores correlacionados con el éxito de la introducción y el carácter invasivo de las aves, y su relación con el tejedor *Ploceus cucullatus* (VW). Los factores indicados en la primera columna muestran correlación con el éxito de la introducción o invasión. En la segunda columna, los números que figuran a continuación de KL corresponden a estudios cuantitativos que verifican cada factor (número de estudios que ofrecen un resultado significativo / número total de estudios), adaptado de KOLAR & LODGE (2001b) y adaptaciones subsiguientes (según SOL, 2001; KOLAR & LODGE, 2001a). Es posible que dichos estudios no constituyan ensayos independientes de la hipótesis, dado que cuatro de los ocho estudios presentados corresponden a aves de Nueva Zelanda. Las otras iniciales de la segunda columna se refieren a los siguientes estudios: LMA. LOCKWOOD et al. (1993); C. CASE (1996); SMC. SORCI et al. (1998); MMS. McLAIN et al. (1999); BD. BLACKBURN & DUNCAN (2001); STL. SOL et al. (2002). En ningún caso dos estudios ofrecen resultados significativos opuestos entre sí; <sup>1</sup> CASE (1996) midió en realidad el número de extinciones de especies nativas, pero la consideró una variable sustitutiva para el "grado de actividad humana y destrucción y deterioro del hábitat..."; <sup>2</sup> LOCKWOOD et al. (1993) midieron en realidad la sobredispersión morfológica de las especies introducidas con respecto a las especies nativas, al considerarla como un indicador de competencia; <sup>3</sup> Los dos estudios significativos obtienen resultados diversos (SOL, 2001); <sup>4</sup> BLACKBURN & DUNCAN (2001) midieron en realidad la diferencia de latitud y la proporción de introducciones en una misma región biogeográfica como la población de origen, pero lo consideraron como una variable sustitutiva para las "características climáticas y de hábitat"; <sup>5</sup> Ningún estudio cuantitativo ha comprobado si las aves exóticas establecidas o con éxito en su acción invasiva tienden a establecerse o convertirse en invasivas del mismo modo en introducciones subsiguientes. El factor está incluido aquí por su plausibilidad (SIMBERLOFF & BOECKLEN, 1991; VERMEIJ, 1996).*

	Studies	Consistent with VW?	Comments regarding probable influence on VW introduction and invasion success
<b>Extrinsic Factors</b>			
<b>Introduction success</b>			
More individuals released	KL 8/8	no	Introductions most likely from scapes, propagule size small
More introduction events	C, KL 5/7	yes	Several recent sightings in Europe and New World; active trade
Biogeographic region	BD	yes/no	Palaearctic high success/Nearctic low (Caribbean intermediate)
More human activity <sup>1</sup>	C	yes	VW associates with human settlement and agriculture (see text)
Less intersp. competition <sup>2</sup>	LMA	?	Competitors widespread; but VW a fierce competitor (see text)

Table 1. (Cont.)

		Consistent Studies with VW?	Comments regarding probable influence on VW introduction and invasion success
<b>Invasiveness</b>			
More individuals released	KL 1/1	no	Introductions most likely from escapes, propagule size small
More introduction events	KL 1/1	yes	Several recent sightings in Europe and New World; active trade
<b>Intrinsic Factors</b>			
<b>Introduction success</b>			
Higher body mass	KL 2/5 <sup>3</sup>	no	VW small (mass 31–45 g) (MACLEAN, 1985)
Plumage monomorphism	MMS, SMC, STL	no	VW conspicuously dimorphic
Lack of migration	KL 1/4	yes	VW not known to migrate (CROOK, 1963; ADEGOKE, 1983a; PARKER, 1999)
More broods per season	KL 1/2	yes	VW breeding season 3–12 months (CYRUS & ROBSON, 1980; BARRÉ & BARAU, 1982; CRAIG, 1997). Mean four breeding attempts in a 75–day period (DA CAMARA–SMEETS, 1982)
Higher nest site	MMS	yes	VW usually nests 2–15m high throughout range (pers. obs.)
Broader diet	MMS	yes	VW will eat seeds and insects (ADEGOKE, 1983a); will also eat fruit (pers. obs.)
Commensalism with humans	STL	yes	VW associates with human settlement and agriculture (see text)
Larger geographic range size	BD	yes?	Introduced birds range from 0.25 to 68,625 degrees <sup>2</sup> , mean 1386 (T. M. Blackburn, pers. comm.). VW range ~3715 degrees <sup>2</sup> .
Better habitat/climate match	BD <sup>4</sup> , KL 1/1	yes	E.g., West Indies, southern U.S., and Mediterranean (see text)
Successful introduction history <sup>5</sup>		yes	Established in three of three known introductions; but failed introduction events (escapes) may go unnoticed.
<b>Invasiveness</b>			
Presence of migration	KL 1/1	no	VW not known to migrate (CROOK, 1963; ADEGOKE, 1983a; PARKER, 1999)
Smaller body mass	KL 1/1	yes	VW small (mass 31–45 g) (MACLEAN, 1985)
Smaller egg mass	KL 1/1	yes	VW small (mass 2.3–3.6 g, <i>N</i> = 94 clutches)
Shorter juvenile period	KL 1/1	?	Juvenile period uncertain for VW
More broods per season	KL 1/1	yes	VW breeding season 3–12 months (CYRUS & ROBSON, 1980; BARRÉ & BARAU, 1982; CRAIG, 1997). Mean four breeding attempts in 75–day period (DA CAMARA–SMEETS, 1982)
Greater longevity	KL 1/1	?	Longevity uncertain for VW
Better habitat/climate match	KL 1/1	yes	E.g., West Indies, southern U.S. and Mediterranean (see text)
Successful invasion history <sup>5</sup>		yes	Invasive in three of three known introductions; but at least one noninvasive naturalized population exists.

tion success in birds, 11 are consistent with success of the Village Weaver, at least in some regions of probable introduction. Of eight factors correlated with invasiveness for which relevant information about the Village Weaver exists, six are consistent with the Village Weaver. Intrinsic factors strongly favor both introduction success and invasiveness. The only thorough exception to this is plumage dimorphism, although migratory behavior and body mass appear to have opposite effects on introduction success versus invasiveness. The contribution of extrinsic factors is more ambivalent. The pattern of introduction is likely to consist of common releases of a very small number of individuals, and the likelihood of success also varies with the region of introduction. Two factors whose contribution is complex will be described in more detail: habitat and climate match, and competition.

#### Habitat and climate requirements

Successful introductions are associated with similarity of habitat and climate between the area of introduction and that to which the bird species is adapted (KOLAR & LODGE, 2001b; BLACKBURN & DUNCAN, 2001). Although general indicators are quantitative and convenient, such as latitudinal differences and proportion of introductions in the same biogeographic region (BLACKBURN & DUNCAN, 2001), each bird species is likely to have particular habitat or climatic limitations. Among these can be elevation, ecosystem type, temperature, and precipitation.

The Village Weaverbird is not usually found above 300 m in elevation (CHEKE, 1987; personal observation), although CLANCEY (1964) reports it to exist up to 1500 m in KwaZulu-Natal, South Africa. Its tendency to be a lowland bird is especially evident on volcanic islands to which it has been introduced, such as Mauritius where even irrigated agricultural fields on the central plateau were devoid of colonies in early 2001. Elevation is below 300 m in nearly all of the American southeast up to the Appalachians, and on several islands near Hispaniola, particularly Cuba. Large tracts of land exist within the Village Weaver's accustomed elevation range in the western and southern portions of the Iberian peninsula. Italy, tends to be more mountainous, which suggests that a naturalized population of the Village Weaver there might be more localized.

Landscapes converted from natural ecosystems to either development or agriculture are more likely to contain introduced birds (CASE, 1996). Village Weavers in particular exhibit diversity in their preference of ecosystem type. Their broad distribution in subsaharan Africa indicates the habitat generalism of this species (BATES, 1930). However, several generalizations hold throughout their range. On a local scale, they are most abundant near agricultural fields and water sources (BANNERMAN, 1949; CYRUS & ROBSON, 1980;

MACLEAN, 1985; RAFFAELE et al., 1998; LAHTI & LAHTI, 2002). The Village Weaver is particularly noted for its tendency to dwell among human habitations, from which it may gain some protection from predators (BATES, 1930; MOREAU, 1942; DA CAMARA-SMEETS, 1982; BARRÉ & BARAU, 1982; LAHTI et al., 2002). For example, BATES (1909) writes, "No sooner is a clearing made and stakes set in the ground for a new village than 'Benga'a' begin to build in the nearest tree...The more populous the village and the greater the hubbub of village life, the better are the birds pleased". They avoid dense forests, although they can be found in small woodlots or forests open enough to permit grasses. Trees are preferred for nesting, although in areas of abundant food (e.g. near ricefields) they occasionally nest in shrubs or even herbaceous vegetation (personal observation). The Village Weaver's preference for disturbed or agricultural lands is reflected in its reported range expansion in Africa over the last century, "due to the opening up of forests through increasing desiccation, fire, the relentless spread of human cultivation and the concomitant encroachment of savannah into what was previously homogenous forest land" (CROOK, 1963: 222). Based on these habitat preferences, the Village Weaver seems well suited to Cuba and much of the southeastern U.S. (especially Florida, whose land is almost completely converted to development or agriculture). By the same considerations the largely agricultural European countries of Spain and Portugal, as well as southern France and Italy, provide appropriate Village Weaver habitat (data obtained from USDA NRCS-NATURAL RESOURCES CONSERVATION SERVICE, 1992; SEI-STOCKHOLM ENVIRONMENT INSTITUTE, 1999).

The Village Weaver is a tropical to subtropical species, so temperature may be a factor governing its distribution. A comparison of the Village Weaver's current global distribution with average annual temperatures and minimum annual temperatures of 30 cities in and near the bird's range (NOAA-NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION, 1991) reveals that the Village Weaver tends to exist only near cities where the average annual temperature exceeds 20°C, and only where the minimum annual temperature is above 0°C. However, the Village Weaver has recently expanded its range into the vicinity of Gabarone, Botswana (PETERSEN, 1991; HERREMANS et al., 1994), where the minimum annual temperature does dip below freezing (-2°C in 2001). If temperature is a range-limiting factor in this species, various areas in the southern U.S.A. (southern half of Florida, south Texas, southwestern Arizona, and the coast of California), and the Caribbean Islands fit the weaver's accustomed average and minimum annual temperature regime (CPC-CLIMATE PREDICTION CENTER, 2002). In general the coastal areas of Spain and Portugal, the southern coast of France, and portions of the Italian coast (particularly near the French border and in the south) are also warm enough. Much of

the interior of these countries, however, including Spain, dip readily below freezing. Nevertheless, an attitude of caution is still warranted in colder areas. The average annual temperature in Los Angeles, CA, U.S.A. is below 20°C, yet Village Weavers have survived for years in aviaries there with no climate control, exhibiting no apparent variation in behavior with temperature fluctuation, except for more resting at higher temperatures (COLLIAS et al., 1971). Moreover, temperature does not explain the absence of the weaver from many areas near its range which do have appropriate temperatures, such as much of Somalia, South Africa, and the northern Sahel.

The length of the rainy season determines the length of the Village Weaver's breeding season (DA CAMARA-SMEETS, 1982). In fact, in the moister areas of Africa they breed in every month of the year and the males might never molt into their nonbreeding plumage (CHAPIN, 1954). There is evidence that rain is important in initiating colonies, and partly also in establishing subsequent breeding synchrony within the colony (HALL, 1970). Not surprisingly, therefore, precipitation provides a more accurate indicator of the range of the Village Weaver than temperature. For instance, a map of the Village Weaver's range in Africa coincides at all borders with a map of the areas which receive at least a millimeter of rain per day on annual average (GPCP-GLOBAL PRECIPITATION CLIMATOLOGY PROJECT, 2000). The precipitation contour explains, for instance, the Village Weaver's range in Southern Africa, which skirts Namibia and most of Botswana and terminates in a finger curving along the eastern coast of South Africa. It also explains the weaver's absence from the region of Somalia southeast of the Red Sea, as well as the drier latitudes of the continent north of about 15°N. Comparing this one mm/day rule with the regions of probable introduction, all of the areas fit this criterion except for the far west of Mexico and the United States. Captive Village Weavers, of course, may breed all summer regardless of rainfall if provided with food, water and nesting materials by caretakers (COLLIAS & COLLIAS, 1970). Likewise, in the uncommon case in nature where a dependable food and water supply and drought-resistant vegetation persist despite a lack of rainfall, Village Weavers may breed where they would not otherwise be expected. For example, in the Dominican Republic in V-VI 2001, weavers were observed breeding in large colonies in the northwestern desert, where the watercourses were completely dry and where no rain fell for at least a month, but where juicy cactus fruits were available and regularly consumed (personal observation).

Several areas of Europe and North America, then, in addition to the Caribbean, apparently provide appropriate climate and habitat for the Village Weaver, according to comparisons of elevation, ecosystem type, temperature and precipitation. Specifically, Florida and the Gulf Coast, much of Portugal, lowlying areas of Spain, southern France, and the northwestern and southern coastal areas of Italy fit the Village Weaver's

current range in all these respects. Moving inland or northward from these areas tends to compromise one or more of the factors.

### Competition

Evidence suggests that competition with other introduced species may affect introduction success (LOCKWOOD et al., 1993). This is difficult to test adequately (SIMBERLOFF & BOECKLEN, 1991), and is likewise difficult to assess for any given species or region of probable introduction. With regard to the Village Weaver in particular, introduction success in the Mascarenes in the 1880's would have been considered unlikely according to the competition hypothesis, due to the high numbers of introduced species that already existed on those islands (MOULTON et al., 1996). Despite competition, and despite a small propagule size, both introductions succeeded. Nevertheless, Village Weavers may yet encounter and be affected by competitors whose effects on their population size and invasiveness are difficult to predict.

The Village Weaver forms large foraging flocks and nesting colonies, and is often involved in synchronized competitive actions such as displacing other bird species in foraging areas and mobbing intruders near and within colonies (personal observation). Individually also they are aggressive, appropriately called "chasers and fighters" in one study (DIN, 1992). The individual sighted in North Carolina was observed supplanting a Boat-tailed Grackle (*Quiscalus major*), a species over twice as long, at a feeder (HIPPI, 1988). Together with its compact and enclosed nest structure, aggression in this species functions as a defense against enemies such as brood parasites or predators (COLLIAS & COLLIAS, 1964; MACDONALD, 1980; DIN, 1992). These aggressive or competitive characteristics of the Village Weaver may function to enhance its establishment and population growth in new areas.

### **Agricultural pest status**

The extent of concern due to a potential invasive species and the necessity for proactivity depend not only on the species' likelihood of establishment and spread, but also on its probable ecological or environmental impact. The Village Weaver's habits of nesting in raucous colonies and denuding the vegetation have been troublesome in Africa (BATES, 1930; CHAPIN, 1954; personal observation). There are also likely to be ecological effects of invasion that do not directly affect human economies. However, by far the most important and immediate concern in areas with Village Weaver populations is the effect of the bird's foraging in agricultural areas. From the earliest accounts of its behavior the species has been known as a destroyer of cereal crops in Africa (BATES, 1909; 1930) and Réunion (BERLIOZ, 1946). Recent accounts of

Table 2. Expected ratings of concern for invasion, according to the Smallwood–Salmon Rating System (SMALLWOOD & SALMON 1992). Values in the interior of the table range from 0 to 1, with a high score representing a high rating of concern in the respective area. Total values (bottom row) range from 9 to 27, with high scores denoting species of generally high concern as invaders. Other known invasive species are provided for comparison with the Village Weaver.

Tabla 2. Índices de preocupación previstos con respecto a la invasión, según el sistema de valoración de Smallwood–Salmon (SMALLWOOD & SALMON 1992). Los valores incluidos en la tabla oscilan entre 0 y 1, donde una puntuación alta representa un alto índice de preocupación en el área respectiva. Los valores totales (fila inferior) oscilan entre 9 y 27, refiriéndose las puntuaciones altas a especies que sugieren una alta preocupación en términos de invasión. También se facilitan otras especies invasoras conocidas, a efectos de establecer una comparación con el tejedor.

	Village Weaver	Pig	House Mouse	Monk Parakeet	House Sparrow	Starling	Quelea
Introduction	0.6	0.82	0.93	0.89	0.64	0.57	0.37
Establishment	0.75	1	1	0.75	1	1	0.25
Damage	0.75	0.89	0.84	0.64	0.66	0.81	0.72
Uncontrollability	0.84	0.43	0.41	0.54	0.41	0.41	0.84
Total rating	27	27	27	27	27	26	21

the species in both its native and introduced ranges nearly always mention the damage it causes to local agriculture (e.g., JENSEN & KIRKEBY, 1980; MICHEL, 1992; RAFFAELE et al., 1998). This dietary preference has been supported by analysis of stomach contents, mainly in West Africa (CHAPIN, 1954; ADEGOKE, 1983a; MANIKOWSKI, 1984; personal observation). A recent survey of more than sixty evaluations of crop damage due to birds in West Africa has concluded that the Village Weaver is in some areas the single worst avian pest, and takes second place in the region as a whole, after the Red-billed Quelea (MANIKOWSKI, 1984). It is the biggest threat to agriculture in The Gambia, where a third of some farmers' rice crops have been destroyed (LAHTI & LAHTI, 2000). It has also been called the worst avian pest in Mauritius (BARRÉ & BARAU, 1982), and in Haiti, where losses of 20–35% to rice are sustained because of this species (BRUGGERS, 1983). An adult consumes on average 250 g of cultivated seeds in 30 days; one thousand birds therefore consume a third of the production of a typical Chadian field of sorghum in one month (DA CAMARA–SMEETS, 1981).

An exception is South Africa, where the species is not considered a major pest (CRAIG, 1997). There are also regions such as central Uganda where weaver damage to crops has been relatively light (KASOMA, 1987). Determining the correlates of such variation in crop damage could provide a basis on which to predict its probable impact in new areas. For instance, neither central Uganda nor eastern South Africa raise rice or similarly sized grains as a major crop, whereas a study in Nigeria found that rice was the most

significant element in the bird's diet when available (ADEGOKE, 1983a). In fact, consistent availability of suitable grains, especially in the breeding season, is suggested to be the factor limiting the size of Village Weaver populations, and in turn, agricultural damage (DA CAMARA–SMEETS & MANIKOWSKI, 1981; ADEGOKE, 1983a).

### Smallwood–Salmon rating system

SMALLWOOD & SALMON (1992) developed a rating system for invasive species which has been used to corroborate California's "most unwanted exotic species" list. The system utilizes questions about a species' invasive history and environmental impact to derive a series of values between 0 and 1 which estimate the relative probability of introduction, establishment, damage, and resistance to control methods. The Village Weaver's scores place it among the most dangerous invasive species, having the maximum total score of 27 (table 2). These values, bolstered with the results of the application of recent studies, permit some bold suggestions. The Village Weaver may be predicted to have the Red-billed Quelea's (*Quelea quelea*) resistance to control, yet nearer to the Starling's (*Sturnus vulgaris*) ease of introduction and establishment. No other exotic bird or mammal species in or near North America has this combination of strengths according to this rating system (SMALLWOOD & SALMON, 1992). The rating system has not yet been applied in the literature to many species in or near other regions.

The rating system's final score results from a double weighting of establishment, and a triple



weighting of damage and uncontrollability. Therefore, the post-invasion impact of the species, regardless of its likelihood of introduction or invasion, is responsible for two thirds of the final score. Since the weaverbird is such a pest in its native range, the system may have inflated the invasiveness potential of this species on that basis. If an effective method were developed for control of the species, the adjustment to the final score would decrease it to 24. Nevertheless, the system is robust to changes in certain parameters: if the questions were answered such that the weaverbird was estimated to be two-thirds as damaging, or half as uncontrollable, the final score would not change.

### Suggestions for prevention and control

In light of the agricultural impact of the Village Weaver and its likelihood of invasion, proactive measures seem in order. Regulating the international trade of these birds is probably the best strategy (BROSSET, 1985). Control methods such as fire, scarecrows, rattles, shooting, nest-robbing, and the felling of trees have not met with much success in Africa, the Mascarenes, or Hispaniola. Poison has been too expensive for most areas and is at best temporary anyway since local birds are responsible for most agricultural damage, and roaming populations can quickly fill in the gaps created by culls (LONG, 1981; ADEGOKE, 1983b). Matters do not seem to have improved in this respect since BATES (1909: 44) noted that "the number killed by man does not seem to affect the population of the colonies. Killing numbers of them will not frighten them away, and tearing down their nests only makes them build the more furiously."

The introduction history of this species suggests that, even where there is a population boom, there is a preceding period of lag (SAKAI et al., 2001) where population sizes are low and probably more manageable. Therefore, in areas where new breeding colonies are reported, proactive control methods, perhaps including removal of the population, may be advisable.

Given the Village Weaver's reliance on rain, those concerned with invasion might use rainfall and breeding season data from the species' current range to predict breeding seasons in new areas. For instance, Portugal receives very little rain between June and September, so Village Weavers introduced to that country will not be likely to breed during that time period. In general the one mm/day rule that on an average annual basis accords well with the species' range, also broadly matches the bird's breeding season when calculated on an average monthly basis (GPCP-GLOBAL PRECIPITATION CLIMATOLOGY PROJECT, 2000). This information can be useful in predicting what areas are likely to have longer breeding seasons, and therefore perhaps higher

population growth, than others; it can also aid in maximizing efficiency of control methods in the event that they are required. Recall, however, that the provision of water and other resources to the weavers (e.g., by humans) can lead to an extension of their breeding season despite a lack of rain (COLLIAS & COLLIAS, 1970).

Much has been written on the pest status and control prospects of the top African bird pest, the Red-billed Quelea (e.g. MANYANZA, 1983; ALLAN, 1983; BRUGGERS & ELLIOTT, 1989). Since this species has similar behaviors and agricultural impacts to the Village Weaver, building upon this research base and appropriating its results may aid in preparedness and control efforts for the more invasive Village Weaver.

### Acknowledgments

For aid in research and the formation of ideas I thank April R. Lahti and Robert B. Payne. For helpful comments I am grateful to Shannon Bouton, John Carroll, Beverly Rathcke, Sheila Schueller, Lindsay Whitlow, and an anonymous referee. Personal communications cited in this article were received from Tim M. Blackburn (School of Biosciences, University of Birmingham, Birmingham, U.K.), Robin Restall (Phelps Ornithological Collection, Caracas, Venezuela), and James W. Wiley (Maryland Cooperative Fish and Wildlife Research Unit, University of Maryland Eastern Shore, Princess Anne, MD, U.S.A.).

### References

- ADEGOKE, A. S., 1983a. Diet of the village weaver *Ploceus cucullatus*. *Malimbus*, 5: 79–89.
- 1983b. The pattern of migration of village weaverbirds (*Ploceus cucullatus*) in southwestern Nigeria. *Auk*, 100: 863–870.
- ALLAN, R., 1983. The strategy for protecting crops from the depredations of quelea birds in Kenya. In: *Proceedings of the Ninth Bird Control Seminar*: 307–316. Bowling Green State University, Bowling Green, OH.
- BANNERMAN, D. A., 1949. *The Birds of Tropical West Africa, Volume 7*. Oliver and Boyd, Edinburgh.
- BARLOW, C., WACHER, T. & DISLEY, T., 1997. *A Field Guide to the Birds of The Gambia and Senegal*. Pica Books, Mountfield, U.K.
- BARRÉ, N. & BARAU, A., 1982. *Oiseaux de la Réunion*. Imprimerie Arts Graphiques Modernes, St. Denis, France.
- BARRÉ, N. & BENITO-ESPINAL, E., 1985. Oiseaux granivores exotiques implantés en Guadeloupe, à Marie-Galante et en Martinique (Antilles françaises). *L'Oiseau et la Revue Française d'Ornithologie*, 55: 235–241.
- BATES, G. L., 1909. Field-notes on the birds of southern Kamerun, West Africa. *Ibis*, 3 (9th

- Series): 1–74.
- 1930. *Handbook of the Birds of West Africa*. John Bale, Sons, & Danielsson, London.
  - BERLIOZ, J., 1946. *Oiseaux de la Réunion*. Librairie La Rose, Paris.
  - BLACKBURN, T. M. & DUNCAN, R. P., 2001. Determinants of establishment success in introduced birds. *Nature*, 414: 195–197.
  - BOND, J., 1936. *Birds of the West Indies*. The Academy of Natural Sciences of Philadelphia, Philadelphia, PA.
  - BROSSET, A., 1985. Construction de nids par un Tisserin gendarme (*Ploceus cucullatus*) sur l'Étang de Saclay (France). *Alauda*, 53: 231.
  - BRUGGERS, R. L., 1983. Senegal's trade in cage birds. In: *Proceedings of the Ninth Bird Control Seminar*: 321–323 (Ed.) Bowling Green State University, Bowling Green, OH.
  - BRUGGERS, R. L. & ELLIOTT, C. C. H., 1989. *Quelea quelea: Africa's Bird Pest*. Oxford University Press, Oxford.
  - CASE, T. J., 1996. Global patterns in the establishment and distribution of exotic birds. *Biological Conservation*, 78: 69–96.
  - CHAPIN, J. P., 1954. The Birds of the Belgian Congo, part 4. *American Museum of Natural History Bulletin*, 75.
  - CHEKE, A. S., 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. In: *Studies of Mascarene Island Birds*: 5–89 (A. W. Diamond, Ed.) Cambridge University Press, Cambridge, U.K.
  - CLANCEY, P. A., 1964. *The Birds of Natal and Zululand*. Oliver and Boyd, Edinburgh.
  - COLLIAS, N. E. & COLLIAS, E. C., 1964. Evolution of nest-building in the weaverbirds (Ploceidae). *University of California Publications in Zoology*, 73: 1–239.
  - 1970. The behavior of the West African village weaverbird. *Ibis*, 112: 457–480.
  - 1971. Comparative behaviour of West African and South African subspecies of *Ploceus cucullatus*. *Ostrich*, Supplement 9: 41–52.
  - COLLIAS, N. E., VICTORIA, J. K., COUTLEE, E. L. & GRAHAM, M., 1971. Some observations on behavioral energetics in the village weaverbird II. All-day watches in an aviary. *Auk*, 88: 133–143.
  - CPC (CLIMATE PREDICTION CENTER), 2002. *Regional Climate Maps*: Ed.) National Center for Environmental Prediction (NCEP), National Weather Service (NWS), and National Oceanic and Atmospheric Administration (NOAA), Washington, D.C., U. S. A.
  - CRAIG, A. J. F. K., 1997. Spottedbacked Weaver. In: *The Atlas of Southern African Birds*, vol. 2: 554–555 (J. A. Harrison, D. G. Allan, L. G. Underhill, M. Herremans, A. J. Tree, V. Parker & C. J. Brown, Eds.) BirdLife South Africa, Johannesburg, South Africa.
  - CRAMP, S. & PERRINS, C. M. (Eds.), 1994. *Handbook of the Birds of Europe, the Middle East and North Africa*, vol. 8. Oxford University Press, Oxford.
  - CROOK, J. H., 1963. Comparative studies on the reproductive behaviour of two closely related weaver bird species (*Ploceus cucullatus* and *Ploceus nigerrimus*) and their races. *Behaviour*, 21: 177–232.
  - CYRUS, D. & ROBSON, N., 1980. *Bird Atlas of Natal*. University of Natal Press, Pietermaritzburg, South Africa.
  - DA CAMARA-SMEETS, M., 1981. Les bilans énergétiques pendant la reproduction du tisserin gendarme, *Ploceus cucullatus*. Nature et importance des prélèvements sur le milieu. *Gerfaut*, 71: 415–431.
  - 1982. Nesting of the village weaver *Ploceus cucullatus*. *Ibis*, 124: 241–251.
  - DA CAMARA-SMEETS, M. & MANIKOWSKI, S., 1981. Preferences alimentaires de *Ploceus cucullatus* au Tchad. *Malimbus*, 3: 41–48.
  - DIN, N. A., 1992. Hatching synchronization and polymorphism in the eggs of *Ploceus cucullatus* and *P. nigerrimus* with data on nest parasitism. *African Journal of Ecology*, 30: 252–260.
  - ELTON, C. S., 1958. *The Ecology of Invasion by Plants and Animals*. Methuen, London.
  - ENSERINK, M., 1999. Biological invaders sweep in. *Science*, 285: 1834–1836.
  - GPCP (GLOBAL PRECIPITATION CLIMATOLOGY PROJECT), 2000. *GPCP Color Precipitation Maps*. World Data Centre for Meteorology, National Climatic Data Center (NCDC), Asheville, N.C., U.S.A.
  - HALL, B. P. & MOREAU, R. E., 1970. *An Atlas of Speciation in African Passerine Birds*. Trustees of the British Museum (Natural History), London.
  - HALL, J. R., 1970. Synchrony and social stimulation in colonies of the blackheaded weaver *Ploceus cucullatus* and Veillot's black weaver *Melanopteryx nigerrimus*. *Ibis*, 112: 93–104.
  - HAZEVOET, C. J., 1995. *The Birds of the Cape Verde Islands*. British Ornithological Union, Tring, U.K.
  - HERREMANS, M., BORELLO, W. & HERREMANS-TONNOEYR, D., 1994. New cases of the spottedbacked weaver *Ploceus cucullatus* breeding near Gaborone. *Babbler*, 26–27: 29–30.
  - HIPP, J., 1988. Village weaver photographed on Seabrook Island, S. C. *Chat*, 52: 81.
  - JENSEN, J. V. & KIRKEBY, J., 1980. *The Birds of the Gambia*. Aros Nature Guides, Aarhus, Denmark.
  - JONES, C., 1996. Bird introductions to Mauritius: status and relationships with native birds. In: *The Introduction and Naturalisation of Birds*: 113–123 (J. S. Holmes & J. R. Simons, Eds.) HMSO, London.
  - KASOMA, P. M. B., 1987. Is the black-headed weaver a pest? *African Journal of Ecology*, 25: 107–116.
  - KOLAR, C. S. & LODGE, D. M., 2001a. Predicting invaders: Response from Kolar and Lodge. *Trends in Ecology & Evolution*, 10: 546.
  - 2001b. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, 16: 199–204.
  - LAHTI, D. C. & LAHTI, A. R., 2000. The village weaverbird: A common bird of uncommonly great concern. In: *Daily Observer*: 11. Banjul, The Gambia.

- 2002. How precise is egg discrimination in weaverbirds? *Animal Behaviour*, 63: 1,135–1,142.
- LAHTI, D. C., LAHTI, A. R. & DAMPHA, M., 2002. Nesting associations of the village weaver (*Ploceus cucullatus*) with other animal species in The Gambia. *Ostrich*, 73: 59–60.
- LE MARÉCHAL, P., 1985. Construction de nids par un Tisserin gendarme (*Ploceus cucullatus*) sur l'Étang de Saclay (France). *Alauda*, 53: 228–231.
- LEVER, C., 1987. *Naturalized Birds of the World*. Longman Scientific & Technical, Harlow, England.
- LOCKWOOD, J. L., MOULTON, M. P. & ANDERSON, S. K., 1993. Morphological assortment and the assembly of communities of introduced passeriforms on oceanic islands: Tahiti versus Oahu. *American Naturalist*, 141: 398–408.
- LONG, J. L., 1981. *Introduced Birds of the World*. Universe Books, New York.
- MACDONALD, M. A., 1980. Observations on the diederik cuckoo in southern Ghana. *Ostrich*, 51: 75–9.
- MACLEAN, G. L., 1985. *Roberts' Birds of Southern Africa*, 5th edition. Trustees of John Voelcker Bird Book Fund, Cape Town, South Africa.
- 1993. *Roberts' Birds of Southern Africa*, 6th edition. Trustees of John Voelcker Bird Book Fund, Cape Town, South Africa.
- MANIKOWSKI, S., 1984. Birds injurious to crops in West Africa. *Tropical Pest Management*, 30: 379–387.
- MANYANZA, D. N., 1983. Quelea control operations in Tanzania. In: *Proceedings of the Ninth Bird Control Seminar*: 317–320. Bowling Green State University, Bowling Green, OH.
- MAYR, E. & GREENWAY, J. C. JR. (Eds.), 1962. *Checklist of Birds of the World, vol. 15*. Museum of Comparative Zoology, Cambridge, MA.
- MCLAIN, D. K., MOULTON, M. P. & SANDERSON, J. G., 1999. Sexual selection and extinction: the fate of plumage-dimorphic and plumage-monomorphic birds introduced onto islands. *Evolutionary Ecology Research*, 1: 549–565.
- MICHEL, C., 1992. *Birds of Mauritius*, 3rd edition. Editions de l'Océan Indien, Rose Hill, Mauritius.
- MOREAU, R. E., 1942. The nesting of African birds in association with other living things. *Ibis*, 6 (14th Series): 240–263.
- MOULTON, M. P., SANDERSON, J. G. & SIMBERLOFF, D., 1996. Passeriform introductions to the Mascarenes (Indian Ocean): An assessment of the role of competition. *Ecologie*, 27: 143–152.
- NAUROIS, R. D., 1994. *Les Oiseaux des Iles du Golfe de Guinée*. Instituto de Investigação Científica Tropical, Lisbon, Portugal.
- NOAA (NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION), 1991. *Climates of the World*. National Climatic Data Center, Asheville, N.C., U.S.A.
- NORTON, R. L., 1989. West Indies region. *American Birds*, 43: 174–175.
- PARKER, V., 1999. *The Atlas of the Birds of Sul do Save, Southern Mozambique*. Avian Demography Unit and Endangered Wildlife Trust, Cape Town and Johannesburg, South Africa.
- PETERSEN, S. E., 1991. Spottedbacked Weaver *Ploceus cucullatus* breeding at Gaborone Dam. *Babbler*, 21–22: 74–76.
- PEZZO, F. & MORELLINI, M., 1999. Breeding attempt of the village weaver, *Ploceus cucullatus*, at Montepulciano Lake (Sienna, central Italy). *Rivista Italiana di Ornitologia*, 69: 142–145.
- PINCHON, R. & BENITO-ESPINAL, E., 1980. Installation de nouvelles espèces à la Martinique. *L'Oiseau et la Revue Française d'Ornithologie*, 50: 347–348.
- RAFFAELE, H., WILEY, J., GARRIDO, O., KEITH, A. & RAFFAELE, J., 1998. *Birds of the West Indies*. Christopher Helm, London.
- SAKAI, A. K., ALLENDORF, F. W., HOLT, J. S., LODGE, D. M., MOLOFSKY, J., WITH, K. A., BAUGHMAN, S., CABIN, R. J., COHEN, J. E., ELLSTRAND, N. C., MCCAULEY, D. E., O'NEIL, P., PARKER, I. M., THOMPSON, J. N. & WELLER, S. G., 2001. The population biology of invasive species. *Annual Review of Ecology and Systematics*, 32: 305–332.
- SEI (STOCKHOLM ENVIRONMENT INSTITUTE), 1999. *Land Cover Map of Europe*. University of York, York, U.K.
- SIMBERLOFF, D., 1992. Extinction, survival, and effects of birds introduced to the Mascarenes. *Acta Oecologica*, 13: 663–678.
- SIMBERLOFF, D. & BOECKLEN, W., 1991. Patterns of extinction in the introduced Hawaiian avifauna: a reexamination of the role of competition. *American Naturalist*, 138: 300–327.
- SMALLWOOD, K. S. & SALMON, T. P., 1992. A rating system for potential exotic bird and mammal pests. *Biological Conservation*, 62: 149–159.
- SOL, D., 2001. Predicting invaders. *Trends in Ecology & Evolution*, 16: 544.
- SOL, D., TIMMERMANS, S. & LEFEBVRE, L., 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour*, 63: 495–502.
- SORCI, G., MØLLER, A. P. & CLOBERT, J., 1998. Plumage dichromatism of birds predicts introduction success in New Zealand. *Oikos*, 90: 599–605.
- USDA NRCS (NATURAL RESOURCES CONSERVATION SERVICE), 1992. *Dominant Cover/Use Types*. Natural Resources Inventory (NRI), Washington, D.C.
- VERMEIJ, G. J., 1996. An agenda for invasion biology. *Biological Conservation*, 78: 3–9.
- WAVER, R. H., 1996. *A Birder's West Indies: An Island-by-Island Tour*. University of Texas Press, Austin.
- WETMORE, A. & SWALES, B. H., 1931. The birds of Haiti and the Dominican Republic. *U.S. Museum of Natural History Bulletin*, 155: 1–459.
- WILLIAMSON, M. H., 1996. *Biological Invasions*. Chapman and Hall, London.