

# EVOLUTIONARY TRENDS AND EXTREME CASES OF LIFE HISTORY TRAITS IN THE CANARY ISLAND BLUE TIT *CYANISTES TENERIFFAE* ON OCEANIC ISLANDS (CANARY ISLANDS)

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**SUMMARY.**—*Evolutionary trends and extreme cases of life history traits in the Canary Island blue tit Cyanistes teneriffae on oceanic islands (Canary Islands).*

**Aims:** In order to discern principal evolutionary trends in the Canary Island blue tits (*Cyanistes teneriffae*) this study provides the first comprehensive description of the main life history traits for this passerine bird in the most important habitat types (laurel forest, pine forest and *Phoenix / Tamarix* community) on two contrasting islands (i.e. Tenerife and Fuerteventura).

**Location:** one study site on pine forest and laurel forest of Tenerife and one location on *Phoenix / Tamarix* on Fuerteventura (Canary Islands).

**Methods:** 250 nestboxes were monitored from December to July (2000 - 2004) and the following parameters were collected: the date of laying (i.e. day of first egg), clutch size (number of eggs laid in a clutch), breeding success (hatched young-dead in nest/eggs laid x 100), second clutches (laid in the same nestbox from which a brood of young had already fledged successfully), percentage of second clutches (number of females that laid a second clutch/ number of females that laid a first clutch x 100). Data on nestling weights were obtained daily in the laurel forest of Tenerife during the breeding season of 2002. In the pine forest of Tenerife (year 2002) birds were caught in the boxes when nestlings were *c.* 8 days old. These were aged in two classes: first year and older birds, based on plumage characteristics.

**Results:** When compared with data across the entire range, the Canary Island blue tit was similar in weight and growth pattern, but revealed extreme cases of life-history traits such as the earliest mean laying date (3 February, Fuerteventura), the lowest mean clutch size ( $4.0 \pm 0.88$  eggs, Tenerife laurel forest), and the highest percentage of second clutches (40.8 % Tenerife laurel forest).

**Conclusions:** Our study suggests that the laurel forest seems to be the optimal habitat for this species in terms of chick productivity. We provide evidence, inferred from our data, that this low reproductive rate was counterbalanced by high adult survival and greater longevity. Therefore, tits on these islands have evolved trends often found on oceanic islands as a consequence of a severe insular syndrome. This study supports the new taxonomic status of the N African / Canary complex (i.e. Canary Island blue tit *Cyanistes teneriffae*).

*Key words:* Canary Islands, Tenerife, Fuerteventura, Canary Island blue tit, por *Cyanistes teneriffae teneriffae*, *Cyanistes teneriffae degener*, *evolutionary trends*, *life-history traits*, *laying date*, *clutch size*, *breeding success*, *percentage of second clutches*, *longevity*.

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RESUMEN.—*Tendencias evolutivas y casos extremos de historia de vida en el herrerillo canario* *Cyanistes teneriffae* en islas oceánicas (islas Canarias).

**Objetivos:** Con el fin de discernir las principales tendencias evolutivas en el herrerillo de las islas Canarias (*Cyanistes teneriffae*) este estudio proporciona las descripciones más completas de la historia de la vida para este passeriforme en los hábitats más importantes (laurisilva, pinar y *Phoenix / Tamarix*) en dos islas diferentes (i.e. Tenerife y Fuerteventura).

**Localidad:** un área de estudio en pinar y laurisilva de Tenerife y una localidad en *Phoenix / Tamarix* en Fuerteventura (islas Canarias).

**Métodos:** 250 cajas-nido fueron monitoreadas desde diciembre a julio (2000-2004) y los siguientes parámetros fueron colectados: fecha de puesta (i.e. día de primer huevo), tamaño de puesta (número de huevos en una puesta), éxito reproductor (pollos que eclosionan-pollos muertos en nido/huevos puestos x 100), segundas puestas (puestos en la misma caja donde una puesta ha sido realizada con éxito), porcentaje de segundas puestas (número de hembras que hacen segundas puestas / número de hembra que hacen una primera puesta x 100). Se obtienen datos de pesos de pollos todos los días en la laurisilva de Tenerife durante la época reproductiva del año 2002. En el pinar de Tenerife (año 2002), se capturan los reproductores en las cajas, cuando los pollos tienen una edad aproximada de 8 días. A estos se les asignaron dos clases de edades en base a diferencias en el plumaje: aves de primer año y adultos.

**Resultados:** Al comparar los datos obtenidos con otros en el rango de distribución, el herrerillo canario se asemeja en peso y patrón de crecimiento, pero revela una historia de la vida extrema como la fecha de puesta media más temprana (3 febrero, Fuerteventura), el tamaño de puesta más bajo en promedio ( $4,0 \pm 0,88$  huevos, Tenerife, laurisilva) y el porcentaje más alto de segundas puestas (40,8 % Tenerife, laurisilva).

**Conclusiones:** Nuestro estudio sugiere que la laurisilva parece el hábitat óptimo para la especie, en términos de productividad de pollos. Nosotros aportamos evidencias, inferidas de nuestros datos, de que la baja tasa de reproducción se contrarresta con la alta supervivencia de los adultos y mayor longevidad. Por consiguiente, los páridos de estas islas han evolucionado tendencias típicas de islas oceánicas como consecuencia de un severo síndrome insular. Este estudio apoya el nuevo estatus taxonómico del complejo Norte Africano / Canarias (i.e. herrerillo canario *Cyanistes teneriffae*).

*Palabras clave:* islas Canarias, Tenerife, Fuerteventura, herrerillo canario, *Cyanistes teneriffa teneriffae*, *Cyanistes teneriffae* degener, *tendencias evolutivas*, *historia de la vida*, *fecha de puesta*, *tamaño de puesta*, *éxito reproductor*, *porcentaje de segundas puestas*, *longevidad*.

## INTRODUCTION

How organisms allocate scarce resources to the different stages of their life history (pattern of growth, differentiation, storage and reproduction) is crucial to their fitness, and so evolution (Bennett and Owens, 2002). Explaining the similarities and differences in life-histories as a consequence of variation in ecological conditions is one of the main challenges of ecology (Partridge and Harvey, 1988) and is essential if we are to understand why organisms occur where they do (Southwood, 1988). Islands provide excellent systems with which to address this challenge. In order to recognize evolutionary trends and life-history pat-

terns, the various components of life-histories must be specified.

The biological interest of islands lies in the fact that they represent discrete, variously isolated, fragments of habitat that often owe their faunas and floras to long-distance dispersal from the mainland (Grant, 1998). Described as "natural experiments" by Mayr (1967), many of the most significant advances in evolutionary biology have come through insular observations (e.g., Darwin, 1859; Grant, 1998). Islands differ from continental regions in their degree of isolation, relative size, geological history, reduced taxonomic diversity, degree of endemism, colonization patterns, the degree to which changes have been due to extraneous

influences (Sadler, 1999), and the relative simplicity of insular biotas allows interactions among populations to be deduced which would be obscured in a more complex mainland context (Simberloff, 1974). Islands therefore tend to show evolutionary trends in phenotypic traits such as dispersal, body size, clutch sizes, ecological niche breadth, etc. (Grant, 1998).

The blue tit *Parus caeruleus* (changed recently to *Cyanistes caeruleus* by Gill *et al.*, 2005) ranges over much of the western Palearctic but it also occupies different kind of islands (Cramp and Perrins, 1993). Wallace (1902) defined three types of islands: recent continental islands (e.g., British Islands), old continental islands (e.g., Corsica) and oceanic islands (e.g., Canary Islands). The Canaries are volcanic and true oceanic islands (Wallace, 1902) and it is generally accepted that they have never been connected to the African continent (Kunkel, 1976). Together with the Azores, Madeira, Selvagens and the Cape Verde Is., they form the Macaronesian archipelago. The Canarian archipelago consists of seven major islands and four islets contrasting between the central-western mountainous islands (e.g., Tenerife) to the low semi-desert type eastern islands (e.g., Fuerteventura) closer to the African continent (*c.* 100 km).

Across Europe and North Africa the blue tit has been intensively studied (see references in Fargallo, 2004). However very little is known about this bird on true oceanic islands such as the Canarian island of Tenerife (Grant, 1979), from where small clutch sizes (i.e. 3 - 5 [Lack, 1947; Snow, 1956; Blondel *et al.*, 1987]) and late laying dates (mean first egg: 3 May [Blondel *et al.*, 1993]) have been reported.

Within this taxon (some populations are more distinctive than others and four subspecies, belonging to the *teneriffae* group, have been described for the Canary Islands: *palmen-sis*, La Palma; *teneriffae*, Gomera, Tenerife and Gran Canaria; *ombriosus*, El Hierro; *degener*, Fuerteventura and Lanzarote (Cramp and Perrins, 1993). It has recently been suggested, on

the basis of molecular analysis, that the N African/Canary complex should be treated as a separate species: *Parus teneriffae* (Salzburger *et al.*, 2002; Kvist *et al.*, 2005; Dietzen *et al.*, 2006, 2007), or more appropriate *Cyanistes teneriffae* and a new race has been described for Gran Canaria, *C.t.hedwigii* (Dietzen *et al.* 2007). However, Canarian birds cannot be split from north Africa until further evidence is available (see Kvist, 2006).

This small passerine bird is common in broad-leaved and mixed forests at low and mid-altitudes (Snow, 1954). It prefers oak forests, both 'summergreen' and evergreen wherever they occur, but tends to do less well in evergreen-type habitats e.g. important life-history traits of the blue tit, such as the time of breeding and clutch size, vary enormously depending on whether habitat patches are dominated by deciduous downy oaks (*Quercus humilis*) or evergreen holm-oaks (*Q. ilex*), at least in central Europe (Blondel and Dias, 1994). In the Canary Islands no deciduous forests occur, and tits are more abundant in the evergreen laurel and pine forests (e.g., Tenerife) (Garcia-del-Rey, 2003) but mainly occupy the community of *Phoenix / Tamarix* in the semi-desert type islands such as Fuerteventura (Garcia-del-Rey, 2004; Garcia-del-Rey and Cresswell 2005; Garcia-del-Rey *et al.*, 2006).

Many insectivorous forest birds, such as tits, face considerable spatial and temporal variation in their preferred food supply (i.e. caterpillars) during the breeding season (Perrins, 1965, 1991) and this also varies between habitat types (Tremblay *et al.*, 2003). This constraint can affect important life history traits such as laying date (Perrins, 1970), clutch size (Perrins, 1979) and chick growth and development (Keller and van Noordwijk, 1994). Egg laying must start several weeks before the food supply reaches a maximum (van Balen, 1973) if parents are to have their young in the nest at the best time (i.e. prey numbers peaking when chicks are around 10 days old, when their energy demand peaks). Although examples of both good and bad synchronization have

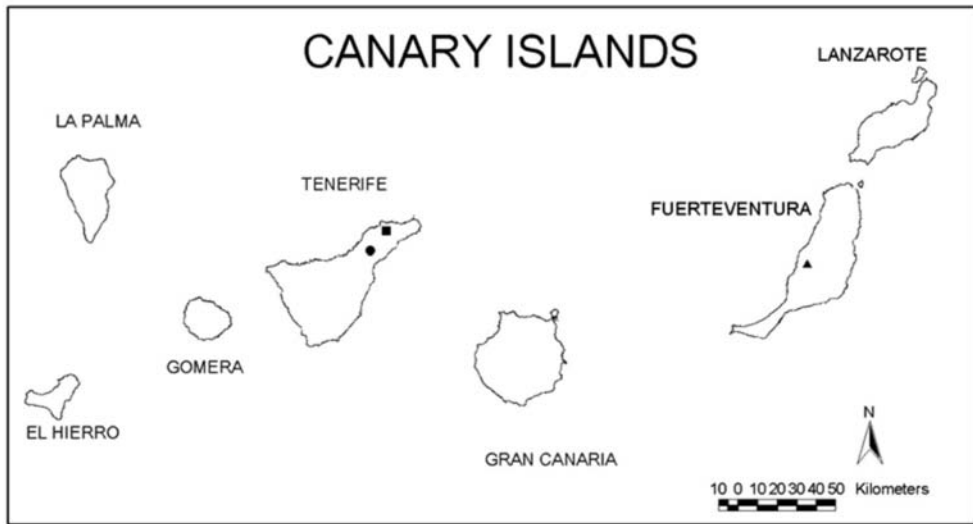


FIG. 1.—Locations of study sites on the Canary Islands (■ = laurel forest, ● = pine forest, ▲ = *Phoenix / Tamarix* community).

[Localización de las áreas de estudio en las islas Canarias (■ = laursilva, ● = pinar, ▲ = Phoenix / Tamarix).]

been observed (Blondel *et al.*, 1992b), in all populations studied the laying pattern found is the same in that eggs are laid well before the caterpillar-peak date.

This study describes, for the first time, the main life history traits (i.e. laying date, clutch size, breeding success, chick growth rate, reproduction and longevity) of the Canary Island blue tit in the dominant habitat types (laurel forest, pine forest and *Phoenix / Tamarix* community) on two contrasting islands (Tenerife and Fuerteventura), and compares these with each other and with similar data from other populations across the species' range in order to discern principal evolutionary trends (a comparative analysis of biometric and diet data from Canary Island blue tits will be presented elsewhere).

#### MATERIALS AND METHODS

This study was conducted in the Canary Islands (27° 37' - 29° 25' N and 13° 20' -18°

10' W): on the islands of Tenerife (2036 km<sup>2</sup>; max height of the island, 3718 m a.s.l.), and Fuerteventura (1662 km<sup>2</sup>; 807 m a.s.l.) during 2000-2004 (see Fig. 1 for locations of study sites).

On Tenerife (28°20' N, 16°20' W), two study sites were chosen in the north-east of the island at similar altitudes to eliminate possible confounding factors (Belda *et al.*, 1998). "Cabezo Zapata" (28°32' N, 16°17' W; 920 m a.s.l.) is an evergreen laurel forest dominated by *Erica arborea*, *Laurus novocanariensis*, *Myrica faya*, *Viburnum tinus*, *Picconia excelsa*, *Persea indica* and *Ilex canariensis*. "Monte Pinar" (28°25' N, 16°23' E; 1250 m a.s.l.) near the town of La Esperanza is a monospecific (planted) pine forest of *Pinus canariensis* with an undergrowth primarily composed of leguminous shrubs and dominated by *Chamaecytisus proliferus*.

On Fuerteventura (28°25' N, 14°06' W), where no natural woods are today present, fieldwork was conducted in *Phoenix / Tamarix* com-

TABLE 1

Number of occupied nests per year on each island (T= Tenerife, F= Fuerteventura) in a particular habitat type ( - = no data available).

[Número de nidos ocupados por año en cada isla (T= Tenerife, F= Fuerteventura) y hábitat particular (- = datos no disponibles).]

	2000	2001	2002	2003	2004	TOTAL
T- Pine forest [ <i>pinar</i> ]	7	33	31	20	14	105
F- Laurel forest [ <i>laurisilva</i> ]	-	20	30	20	-	70
F- <i>Phoenix</i> / <i>Tamarix</i>	6	2	12	8	5	33

munity (Rodríguez *et al.*, 2000). Fuerteventura is a low semi-desert island. The dry gully at La Banda (28°23'N, 14°06'W; 337 m a.s.l.) was selected for the present study. This gully is dominated by Palm trees (*Phoenix sp.*) and Tamarisk (*Tamarix canariensis*). Fruit trees and other exotic plant species (e.g., *Acacia majorera*, *Nicotiana glauca*) grow along the gully. On the mountain slopes there is a low scrub of *Senecio kleinia*, *Euphorbia obtusifolia*, *Asparagus pastorianus* and *Launaea arborescens*.

The climate of this oceanic archipelago is Mediterranean with cool, wet winters and hot, dry summers but is influenced by the local NE trade winds, the proximity to the African Continent (i.e., the Saharan Desert) and the high altitude of the central and occidental islands (Marzol-Jaén, 1984; Volsoe, 1955).

In total, 250 nestboxes were erected on these two islands (see Table 1 for number of occupied nests). All nestboxes (two models: ICONA model C and RSPB inspection box) were distributed along dirt tracks at an approximate distance of 100 m. To eliminate an edge effect, whenever possible, these were located at a perpendicular distance of 50 m from the track. Nest inspection started at the end of December and finished in July. Each nestbox was visited at least every seven days, during the afternoon as tits tend to lay around

dawn (Perrins, 1979), but daily when special measurements were required (e.g., day of hatching). Birds were not disturbed while incubating. All the boxes were cleaned at the end of each field season to remove the nest and to record any dead young left in the nest. For every nest the following parameters were collected: the date of laying (i.e. day of first egg), clutch size (number of eggs laid in a clutch), breeding success (hatched young-dead in nest/eggs laid x 100), second clutches (laid in the same nestbox from which a brood of young had already fledged successfully by a ringed female, when marking was possible), percentage of second clutches (number of females that laid a second clutch / number of females that laid a first clutch x 100; Kluijver, 1951; Perrins, 1979).

Data on nestling weights were obtained daily in the laurel forest of Tenerife during the breeding season of 2002 (i.e. each afternoon around 6:00 pm local time) from the same broods (50 g Pesola spring balance, accuracy 0.1 g) from day 1 to day 15 (Gibb, 1950). The age of the chick was recorded, by casual observation, as 0 on the day of hatching, 1 on the following day, etc.

In the pine forest of Tenerife (year 2002) adult birds were caught and ringed in the boxes when nestlings were *c.* 8 days old. These were aged in two classes: first year and older

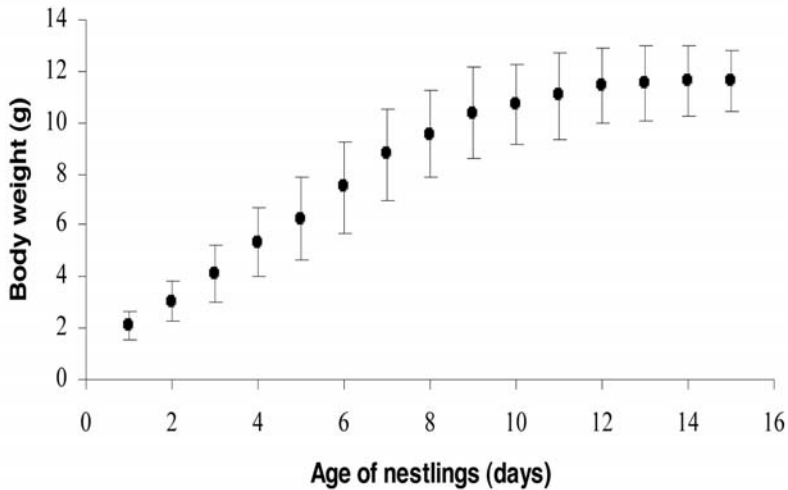


FIG. 2.—Weight (mean of brood means  $\pm$  SD) of Tenerife blue tit (*C. t. teneriffae*) nestlings in relation to age, in laurel forest, 2002 ( $n = 30$  broods of 105 young).

[Peso (media por nidada  $\pm$  DT) de los pollos de herrerillo canario (*C. t. teneriffae*) en relación a la edad (laurisilva), 2002 ( $n = 30$  nidos con 104 pollos).]

birds, based on plumage characteristics (E. Garcia-del-Rey unpub. data). Measurements include wing length (maximum chord), bill length (tip to skull), bill depth (at distal edge of nostril), tarsus (maximum), tail and body mass (Redfern and Clark, 2001). The proportion of juveniles has been used as a measure of adult mortality (Hilden, 1982) and birds were caught also to obtain this ratio.

#### Statistical analysis

Analysis of Variance (ANOVA) was used to test for differences in the average laying date, mean first-clutch size and average breeding success between the three habitat types (dependent variable = laying date, clutch size and breeding success), followed by *post-hoc* Tukey tests.

Due to the lack of data from second clutches in the *Phoenix/Tamarix* on Fuerteventura, inter-habitat testing (i.e. mean laying date

of second clutches and mean second-clutch size) was only possible between the pine and laurel forest on Tenerife and Student t-tests were used for this. Chi-square tests were used to test for differences in the percentage of second clutches. All statistical analyses were performed on SPSS 11.0 and results are presented as mean  $\pm$  standard deviation.

#### RESULTS

##### *Hatching pattern and growth rate*

Although all the eggs within a clutch hatched within a day of each other (obtained by 24 h visits), the nestlings on both Tenerife and Fuerteventura seemed to show an age hierarchy resulting from the small degree of hatching asynchrony. However, this needs to be quantified more precisely.

The overall weight increase of successful young during the nestling period can be seen

TABLE 2

Laying date (1 = 1 January) and clutch size (1 = first, 2 = second clutch), percentage of second clutches (PSC) and breeding success (BS) on Tenerife (T) and Fuerteventura (F) in three habitat types. Means ( $\pm$  SD), sample sizes ( $n$ ) and range in brackets (- = no data available) are also given.

[Fecha de puesta (1 = 1 enero) y tamaño de puesta (1 = primeras y 2 = segundas puestas), porcentaje de segundas puestas (PSC) y éxito reproductor (BS) en Tenerife (T) y Fuerteventura (F) en los tres hábitats estudiados. Media ( $\pm$  DT), muestra ( $n$ ) y rango entre paréntesis (- = datos no disponibles).]

	LD 1	LD 2	CS 1	CS 2	PSC (%)	BS1 (%)	BS2 (%)
T- Pine forest [pinar]	98.1 $\pm$ 15.95 (69 - 136) $n$ = 105	142.0 $\pm$ 11.10 (120 - 157) $n$ = 11	4.2 $\pm$ 0.79 (2 - 6) $n$ = 105	3.5 $\pm$ 0.69 (2 - 4) $n$ = 11	13.09	75.0 (0 - 100) $n$ = 105	60.6 (0 - 100) $n$ = 11
F- Laurel forest [laurisilva]	91.1 $\pm$ 21.05 (52 - 134) $n$ = 70	147.2 $\pm$ 7.84 (130 - 159) $n$ = 21	4.0 $\pm$ 0.88 (2 - 7) $n$ = 70	4.9 $\pm$ 0.59 (4 - 6) $n$ = 21	40.8	63.2 (0 - 100) $n$ = 70	71.6 (0 - 100) $n$ = 21
F- <i>Phoenix</i> / <i>Tamarix</i>	34.37 $\pm$ 20.67 (9 - 85) $n$ = 33	-	5.0 $\pm$ 1.20 (2 - 7) $n$ = 33	-	-	84.20 (0 - 100) $n$ = 33	-

in Figure 2. The rate of growth increased from day 1 until day 10 and then slowed. As this is a similar pattern to that observed elsewhere, where the peak prey demand occurs on about day 10 (van Balen, 1973), this suggests that the maximum food demand required by the nestlings occurs around day 10 in the Canary Islands also.

### Reproduction

An extreme mean laying date for first clutches was found on Fuerteventura (i.e. 3 February, Table 2), which is the earliest ever reported for the species.

Comparing the three study sites, statistically significant differences were observed in the average laying date of first clutches between pine, laurel and *Phoenix* / *Tamarix* community (ANOVA:  $F_{2,205} = 141.9$ ,  $P < 0.001$ ). Laying date was 63.7 days earlier in *Phoenix* / *Tamarix* than in the pine forest (Tukey:  $P < 0.001$ ) and

56.7 days earlier than in the laurel forest (Tukey:  $P < 0.001$ ; see Table 2). No significant difference was observed on Tenerife between the pine and laurel forests for first clutches (Tukey:  $P = 0.51$ ) or second clutches (Student  $t$  test:  $t = -1.61$ ,  $df = 30$ ,  $P > 0.05$ ; Table 2).

The mean size of first clutches (Table 2) differed significantly between the three habitat types (ANOVA:  $F_{2,205} = 15.97$ ,  $P < 0.001$ ). Clutch size was significantly smaller by 0.8 eggs in the pine forest than in the *Phoenix* / *Tamarix* (Tukey:  $P < 0.001$ ) and smaller by 1.0 egg when compared to the laurel forest and *Phoenix* / *Tamarix* (Tukey:  $P < 0.001$ ). No significant difference in mean first clutch size was observed on Tenerife between the pine and laurel forest (Tukey:  $P = 0.29$ ).

The mean second clutch size differed significantly between the pine and laurel forests (i.e. higher by 1.4 eggs on the laurel forest; Student  $t$  test:  $t = -5.74$ ,  $df = 30$ ,  $P < 0.001$ ).

The percentage of second clutches was higher on the laurel forest (40.8 %) than on the pine

forest (13.09 %) but the difference was not statistically significant (Chi-square test:  $\chi^2 = 0.30$ ,  $df = 1$ ,  $P > 0.05$ ).

Neither the breeding success of first broods in the three habitat types (ANOVA, arcsine transformed:  $F_{2,205} = 2.36$ ,  $P > 0.05$ ) nor the breeding success of second broods in the two habitats on Tenerife (Student t test:  $t = -1.0$ ,  $df = 30$ ,  $P > 0.05$ ) differed significantly (Table 2).

### Longevity

The proportion of juveniles has been used as a measure of adult mortality elsewhere (Hilden, 1982; Snow 1956). The first year to adult ratio of breeders (i.e. more than one year old) in the Tenerife pine forest during 2002 was 7:35 ( $n = 42$  birds from 31 nests).

## DISCUSSION

### Growth rate

Each species has a typical growth rate which varies within a certain range (Ricklefs, 1968, 1973), and comparison with populations in the Mediterranean region (Blondel, 1985) and Europe (Gibb, 1950) indicates that the blue tit on Tenerife does not depart from this rule, despite of its recent full species status. The growth constant  $K$  has been used to compare overall growth rates (Ricklefs, 1968, 1973), (i.e.  $K = 1.11 A^{-0.278}$ , where  $A =$  mean adult weights). This exponential relationship describes the dependence of the growth rate in altricial birds on the asymptotic weight. The Tenerife blue tit has an average adult weight of  $A = 10.62 \pm 0.59$  (SD) (sexes combined, year 2002,  $n = 58$ ), which is similar to that of the blue tit in England (Wytham population) *C. c. obscurus*, i.e.  $A = 10.54 \pm 0.67$  (SD) (sexes combined, year 2002,  $n = 496$ ). Therefore, the two species weigh about the same and have a similar growth rate.

### Laying date

The earliest mean lay-date ever recorded for the blue tit was found on Fuerteventura (3 February, this study) and this might be related to the annual patterns of rainfall (Garcia-del-Rey, 2003). The previous earliest laying date reported was observed in southern Spain (21 March; Isenmann *et al.*, 1990). The trend for birds on isolated islands to breed extremely late, suggested by Blondel *et al.* (1993) was not supported by the data in this study. When compared with 87 European populations (Fargallo, 2004), the Tenerife blue tit lays earlier (8 April pine forest, 1 April laurel forest) than the average for the Mediterranean region (i.e. 21 April; Blondel *et al.*, 1993), than the mean for Northern and Central Europe (27 April; Blondel *et al.*, 1993) and than the average for Corsica (12 May; Blondel *et al.*, 1998). Indeed out of 87 populations studied across the range of this species only one shows the same mean laying date (Maicas and Fernandez, 1999).

### Clutch size

The very low clutch size reported by Snow (1956) for the blue tit in Tenerife, is consistent with that found in the present, much more extensive, study. The Fuerteventura blue tit clutch size is even smaller ( $5.0$  eggs  $\pm 1.20$ ) than that of the north African blue tits ( $6.53$  eggs on average from 9 populations; Baouab *et al.*, 1986; Chabi and Isenmann, 1997; Chabi *et al.*, 1995; Isenmann *et al.*, 1982; Moali and Isenmann, 1990) but similar to a population of *P. c. ultramarinus* inhabiting Pantelleria, a small volcanic island between Sicily and Tunisia (Lo Valvo and Massa, 1996). The other Canarian populations also show low first clutch sizes (Garcia-del-Rey, 2003; Garcia-del-Rey *et al.*, 2006).

Outside the western Palearctic similarly low values have been reported for other tit species at southern latitudes:  $4.6 \pm 0.7$  (SD), ash tit



*Parus (Melaniparus) cinerascens*;  $4.1 \pm 0.9$ , carp's tit *P. (Melaniparus) carpi* (both in Africa, Wiggins, 2001) and 3.9 eggs for the varied tit *P. varius* inhabiting an oceanic island near Japan (Higuchi, 1976). The clutch size of the blue tit in the laurel forests of Tenerife is therefore the smallest so far recorded ( $4.0 \pm 0.88$  eggs,  $n = 70$ ). Investigating whether this small clutch size is optimal for the Canary Island blue tit surely merits further study on this oceanic island system.

#### *Percentage of second clutches*

Second clutches are rare in most populations of the blue tit (Perrins, 1979). However second clutches were common on Tenerife on some years (i.e. 40.8 % laurel forest vs 13.09 % pine forest), and commoner than in any population reported by Fargallo (2004), the previous highest being that of 37.5 % in Italy (Bellavita and Sorace, 1991). These two separate reproductive investments in some years may depend on a flat distribution of multiple food resources throughout a prolonged potential breeding season (*unpubl. data*). This has not been observed in continental blue tit populations because they depend mainly on caterpillars with a real pronounced peak.

#### *Laurel forest vs. pine forest*

The importance of the pine forests for the Canarian blue tits has been stressed in the past (Grant, 1979; Lack and Southern, 1949; Partridge and Pring-Mill, 1977; Snow, 1954). However, we found the life-history traits in the first stage of reproduction (i.e. mean laying date of first clutches, first clutch size and breeding success of first broods) to be similar in the populations of the two forest habitat types. The birds do more or less equally well in the first part of the breeding season. However, the mean size of the second clutch is higher in the laurel

forest, suggesting that the feeding conditions are better for females to produce their eggs at that time. As in populations elsewhere, there is clear evidence that early breeding is beneficial, because it allows the possibility of a successful second attempt and thus increases the number of young raised in the year. In most populations studied elsewhere, early raised young have much better options in life than late ones. From this, it appears that the laurel forest is the optimal habitat for this species in the Canary Islands.

This low reproductive rate, in some years, must be counterbalanced by a high survival rate. Elsewhere a typical first-year: adult ratio is 35:42 (45.5 % first-year) equates to an annual survival rate of 83.3 % and an approximate expectation of 5.5 years of further life (Hilden, 1982). However, the first-year: adult ratio of 7:35 (16.7 % first-year) found on Tenerife suggests a significantly greater longevity. Coupled with the low reproductive rate of birds in these populations (compared with the species' productivity elsewhere), this observation suggests that blue tit population in the Canary Islands are relatively K selected. A real survival rate study is needed to confirm what we have observed by a limited method.

#### *Conclusion*

Our results revealed extreme cases of life-history traits for the blue tit on these two oceanic islands (i.e. earliest laying date, lowest clutch size, highest percentage of second clutches), when compared with data from other study sites (Fargallo, 2004).

Evolutionary trends among insular vertebrates can be documented in terms of changes in morphology, ethology, ecology and life-history (Alcover, 2004). Evolutionary change in vertebrates is often linked with insularity (Newton, 1998) through allopatric speciation, and it is generally accepted that they have suffered what has been termed the 'insular syn-

drome' (Blondel, 1986), which can be light, moderate or severe (Alcover, 2004). A severe 'insular syndrome' can affect reproductive parameters by reducing the reproductive rate and recruitment rate but increasing longevity (suggested by this study), an evolutionary trend often found on oceanic islands (Grant, 1998). In the Canaries, the most probable cause of high adult survival (leading to low reproductive investment in some years) could be low predation or low parasite and pathogen pressure.

The blue tit in the Canary Island oceanic archipelago is showing some symptoms of the severe insular syndrome, (evolving changes not found elsewhere): low productivity and high longevity, although they appear to compensate for the low reproductive output by increasing the number of breeding attempts in those years when conditions allow for this, especially in laurel forest. The life-history of a species observed is the result of both long-term selective forces, and of the more immediate responses of an organism to the environment in which it is, and has been, living. The life history information presented here supports the specific recognition of these taxa (i.e. *Cyanistes caeruleus* sensu strictu and *C. teneriffae*).

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