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Seasonal Timing of Reproduction in a Tropical Bird, the Seychelles Warbler: A Field Experiment Using Translocation

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Abstract Reproduction of the Seychelles warbler (*Acrocephalus sechellensis*), a single-island endemic species living close to the equator, is characterized by a pronounced annual rhythm. The bird usually raises only one or two clutches of one egg each per year. Observational data suggest that seasonal changes in feeding conditions are an important proximate factor controlling reproduction. This hypothesis could be tested by transferring breeding pairs from Cousin Island to islands previously unoccupied at the same latitude. These islands, Aride and Cousine, have a higher food supply but similar vegetation and climate. After translocation to Aride Island, with high food availability year-round, individual breeding pairs prolonged their reproductive season (some bred year-round), increased the annual number of broods, and improved the reproductive success per nest-building attempt. Annual production of yearlings per pair on Aride was on average 23 times higher than that of the *same* pair on Cousin before the transfer. After translocation to Cousine Island, where food availability varied seasonally and was intermediate between Cousin and Aride, individual pairs increased the annual number of broods, but reproductive success per nest-building attempt remained the same. Annual production of yearlings per pair on Cousine was on average 5 times higher than that of the *same* pair on Cousin before the transfer. Thus the experiments, controlled for group size, breeding partner, breeder age, and experience, showed that food supply can be an important proximate factor in the timing of reproduction in the tropics. The differences in reproductive timing and success by warblers on the three islands are due not to genetic differences but entirely to differences in environmental conditions.

Key words Seychelles warbler, reproduction, circannual cycles, reproductive timing, feeding condition, food supplementation

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Figure 1. Increase in Seychelles warbler numbers and territories since 1959.

INTRODUCTION

To achieve breeding condition and anticipate an approaching season of good food supplies, birds have evolved response mechanisms to a host of environmental stimuli that function as signals heralding the approach of suitable times. In temperate regions, reproduction takes place during a restricted season when nutritional and climatic conditions for survival of both parents and offspring are optimal. The predominant proximate factors that stimulate endocrine pathways to gonadal development are the seasonal change in day length (Murton and Westwood, 1977) and humidity and water availability (Vleck and Friedkalns, 1985). Although the mechanisms controlling seasonal reproduction in high-latitude birds have been well studied, little is known about proximate cues to reproductive timing in tropical birds. In most species investigated, reproduction is seasonal as it is in temperate zone birds, even in populations living close to the equator. In these regions, day length hardly varies and is, therefore, unlikely to be involved in reproductive timing. Because breeding often is related to the temporal relationship to the rain cycle, it has been suggested that other proximate factors associated with the switch from the dry to the rainy season or vice versa, such as rainfall, temperature, and relative humidity, provide timing cues for these birds. However, experimental evidence supporting these suggestions is almost entirely lacking (Immelmann, 1973; Murton and Westwood, 1977; Gwinner 1986).

In this article, I investigate the constitution of the environmental zeitgebers for annual reproduction in

Figure 2. Map showing the Seychelles Islands with populations of Seychelles warblers: Cousin, Aride as place of first transfer (23-29 September 1988) and Cousine as place of second transfer (29 June to 1 July 1990).

a tropical bird, the Seychelles warbler (*Acrocephalus sechellensis*), a rare endemic known only from the Seychelles Islands. Following long-term management of Cousin Island by BirdLife International since 1968, the warbler population has grown from 26 to about 320 birds in about 115 territories in 1982 (Fig. 1). Until 1988, it occurred only on Cousin (29 hectares), but additional breeding populations were successfully established on the islands of Aride (68 hectares) and Cousine (26 hectares) in September 1988 and June 1990, respectively (Fig. 2) (Komdeur et al., 1991; Komdeur, 1994a, 1996a). The Seychelles warbler is purely insectivorous. Once paired, Seychelles warblers reside permanently in the same territory. The most common clutch size is a single egg (91.1%, $n = 223$). However, females in territories with high food availability can lay larger clutches. Fledging occurs at 18-20 days, and young birds remain highly dependent on adults until they become proficient foragers at about 88 days of age (Komdeur, 1991). Breeding success for warbler pairs was low; only 41.6% of all territories produced independent young, and only 24.7% produced young that survived to 1 year of age. Breeder mortality is low (18.5% per year) and divorce is rare, and so the same pair occupies the same territory for several years, sometimes as long as 9 years. Although warblers can breed successfully in their first year, some individuals remain in their natal territories and delay breeding for several years, sometimes never reproducing. Young frequently remain in their natal territories and act as helpers, aiding in territorial defense, predator mobbing, nest building, incubation (only females), and

feeding dependent young of their parents. Since 1982, cooperative breeding has been widely observed all over the island (Bathe and Bathe, 1982). Removal experiments in the Seychelles warbler have revealed that breeding pairs with one helper have significantly higher reproductive success than do the same breeding pairs after removal of the helper (Komdeur, 1994b). Group living is promoted not only by habitat saturation but also by competition for higher quality territories (Komdeur, 1992).

This study was designed to answer two questions. First, how does seasonal timing of Seychelles warbler reproduction contribute to the prospects of offspring survival? Because most warblers are single-brooded with restricted breeding seasons and have clutches of a single egg, it is expected that the fitness costs of poor timing of breeding are considerable. Should the first breeding attempt fail, there might not always be time available to initiate a replacement clutch. Because the success of a single nesting attempt will determine total seasonal reproductive success, each clutch should be particularly valuable from the parents' point of view. The hypothesis is that the female starts nest building and laying her egg in response to some external cue(s) in such a way that maximum nestling demand roughly coincides with the period of highest food abundance. Second, do Seychelles warblers change their reproductive timing and improve reproductive success when adequate food is available year-round? On Cousin, insect food supply is low with a single annual peak, whereas that on Cousine is medium and that on Aride is high and abundant year-round. On the basis of the translocations, I test the hypothesis that food supply affects reproductive timing and success by comparing breeding performance of the same pairs pre- and posttranslocation under the same climatic conditions.

METHODS

Study Areas and Population

Geologically, Cousin is formed from two distinct parts. The southwestern half consists largely of a steep granite hill (69 m). The northeastern half of the island is flat coastal plain of phosphatic sandstone (Hottinger, 1982). Seasonal climatic variations are determined by changes in the direction and origin of the winds. From about May/June until October/November, a relatively strong (often force 5), steady, southeast trade

wind blows. Between December and March, the northwest monsoon predominates with generally lighter (force 3 to 4) and less persistent winds. Between the two main seasons come transition periods characterized by light winds.

Over the period of 23-29 September 1988, 29 color-ringed adult Seychelles warblers (16 males and 13 females) were transferred from Cousin to Aride by motorboat, a journey of about 45 min. These consisted of 17 experienced birds (which had held a territory and bred at least once), 6 helpers, and 6 nonhelpers. During the 2 years after the transfer, 5 pairs that were breeding pairs on Cousin remained pairs on Aride. During a 3-day period from 29 June to 1 July 1990, 29 color-ringed adult warblers (15 males and 14 females) were transferred from Cousin to Cousine, a journey of about 15 min. These consisted of 16 experienced birds, 9 helpers, and 4 nonhelpers. During the 1 year after the transfer, 4 pairs that were breeding pairs on Cousin remained pairs on Cousine.

On the islands of Cousin and Aride, the warblers were studied simultaneously from September 1988 to November 1991; on Cousine, they were studied from June 1990 to November 1991. On Cousin, all 115-123 territorial groups of the warblers (300-360 birds) were studied from January 1986 to September 1990, 39 groups (139-151 birds) from October 1990 to June 1991, and 35 groups (89-103 birds) from July to November 1991. On Aride, 13-43 groups (29-180 birds) were studied from September 1988 to November 1991. On Cousine, 12-16 groups (29-43 birds) were studied from June 1990 to June 1991 and 10 groups (25-35 birds) from July 1991 to November 1991. Data presented here were based on individually color-ringed birds. As many young as possible were color-ringed. The average yearly percentage of birds that were individually color-ringed was 70% on Cousin, 74% on Aride, and 90% on Cousine.

Breeding Activity

To record breeding activity, all territories on Cousin, Aride, and Cousine were checked every other week for active nests by observing females for 30 min. This observation period was long enough to determine whether birds are breeding; the minimum number of half-minute intervals that a breeding female was involved in either nest building, incubating, or feeding the nestling during this period was 2 (Komdeur, 1991). All nests were checked for clutch size, sometimes with the help of a long stick and angled mirror. Observa-

tions on nest building, incubating, and feeding young were made for 3 h. Feeding observations started in the second week after hatching and were repeated every 3 weeks until the young died or reached independence. For each 30 sec, I noted whether a bird was engaged in any of the behaviors mentioned. All nestlings were individually color-ringed. Fledglings appeared to be nutritionally independent by 3 months of age. Therefore, the probability of reaching independence was measured as the probability of surviving the first 3 months.

Each territory was checked every 2 weeks for the presence of color-ringed birds to determine the proportion of birds that died or survived. Once a bird was missing from its territory, all other territories and vacant areas were checked to assess dispersal. Because emigration from the study area never occurred, I assumed that missing birds had died. On Aride and Cousine, the islands were searched twice a month to plot new territories using a portable tape recorder with a continuous loop cassette of male song to attract birds. Because the three islands have the same habitat types and are close to each other, I employed matched-pairs statistical tests to compare breeding activity and climatical data among them. To isolate group size effects on reproduction, comparisons between breeding performance on different islands were made using warbler pairs only.

Territory Quality and Island Food Abundance

Territory and island quality could be measured in terms of availability of nest sites, density of predators, and/or food availability. Nest sites had no consistent features (within the same territory, nests were found from 1 m to as high as 20 m) and were abundant. Adult Seychelles warblers lack natural predators. Nest predators, Seychelles fody (*Foudia sechellarum*), which are weaver birds endemic to the Seychelles, and two endemic skink species (*Mabuya wrighti* and *Mabuya sechellensis*), were evenly distributed over and equally abundant on the three islands (Brooke and Houston, 1983; Owen, 1986; Komdeur, 1994a, 1996a). Because the warblers are purely insectivorous, taking 98% of their insect food from leaves (Komdeur, 1991), territory and island quality depend on insect prey available and amount of foliage present. The only other insect-eating bird species present on the islands are the Seychelles fody and the endemic Seychelles sunbird (*Nectarinia dussumieri*). In addition, food availability depends on the size of the territory. The quality of all

territories on Cousin was assessed monthly (between the 15th and 29th days) from May 1987 to September 1990. The quality of territories on Cousin and Aride was assessed simultaneously every 3 months (between the 15th and 29th days) from September 1988 to September 1991 and in November 1991; on Cousine, it was assessed every 3 months from June 1990 to September 1991 and in November 1991. Each month (between the 15th and 29th days), island quality of Cousin and Aride was studied from May 1987 to September 1990; island quality of Cousine was studied from August 1989 to September 1990 and every 3 months from November 1990 to November 1991. To determine island quality, insects and vegetation were monitored simultaneously on Cousin and Aride and on Cousine at a later stage at 67, 28, and 20 randomly chosen sites, respectively.

I measured the amount of foliage in each territory and at each site using a transect method. The transect was 250 m long, subdivided into straight subtransects plotted 25 m apart and facing north from one territory boundary to the other. Every 5 m, the presence or absence of foliage and the plant species was noted in the following heights: 0.0-0.75 m, 0.76-2.0 m, 2.1-4.0 m, and 2-m intervals thereafter (for method, see Komdeur, 1991). Total foliage cover for plant species x (c_x) is the total number of cases of presence of foliage at all heights along the transect. To assess prey availability (i_x) in each territory and at each site, I searched the upper and lower sides of 50 leaves per plant species (12 dominant species) for insects. To assess insect density for plant species x , the area of 250 leaves for each species was measured at 50 random sites on the island (5 leaves per site).

Territory quality (Q) was therefore expressed as the mean number of prey invertebrates available within a territory, and mean island quality (F) was expressed as the mean number of prey invertebrates present per site, using the following equations:

$$Q = a \sum_x^{12} (c_x i_x) / 100, \text{ and } F = \sum_x^{12} (c_x i_x) / 100,$$

where a is the mean annual territory size (in hectares), c_x is the mean foliage cover for each of 12 plant species x , and i_x is the mean insect totals for plant species x per unit leaf area (1 dm²) in a territory and on the island, as already described. Territories were divided into three categories: low quality ($Q = 0.0-15.0$), medium quality ($Q = 15.1-30.0$), and high quality ($Q > 30.0$). Monthly insect food increase (FI) during a given

Table 1. Mean annual territory quality ($Q \pm SE$) of control and experimental Seychelles warbler territories during the 2-year period before and after the transfer in 1988 and during the 2-year period before and 1 year after the transfer in 1990.

Territory	Pretransfer	Posttransfer	<i>p</i>
1988			
Experimental (5)	9.2 $\pm$ 2.6	322.8 $\pm$ 89.3	< .0025
Control (7)	10.1 $\pm$ 3.7	8.7 $\pm$ 3.6	n.s.
<i>p</i>	n.s.	< .001	
1990			
Experimental (4)	11.5 $\pm$ 3.1	53.8 $\pm$ 4.1	< .01
Control (6)	13.4 $\pm$ 4.0	12.9 $\pm$ 3.7	n.s.
<i>p</i>	n.s.	< .001	

NOTE: *p* values for territory quality differences between experimental and control territories were determined by two-tailed *t* test, and those within experimental and control territories were determined by paired-sample *t* test. Numbers of territories are in parentheses. n.s. = *p* > .05.

month *n* is calculated as the difference between mean island qualities in month ($n + \frac{1}{2}$) and month ($n - \frac{1}{2}$).

Nutritional Conditions and Reproduction

The translocation of Seychelles warblers and the fact that some breeding pairs from Cousin remained together on the new islands enabled me to measure the influence of food availability on timing and success of reproduction by comparing pretransfer and posttransfer data for the same pairs. The experimental units consisted of 5 Cousin pairs removed to Aride (Experiment 1) and 4 Cousin pairs removed to Cousine (Experiment 2). The control units consisted of 7 and 6 breeding pairs, respectively, on Cousin. In both experiments, the annual reproductive success of each pair was exactly known in the 2 years before and 2 years (Experiment 1) or 1 year after (Experiment 2) the translocation.

All the pairs were experienced breeders because they had bred successfully (i.e., raised fledglings) in 2 consecutive years before transfer. Territory quality, which was correlated with reproductive success (Komdeur, 1991), did not differ significantly between experimental and control territories pretransfer and within control territories during the experimental period (pre- and posttransfer) (Table 1). During the whole experimental period, no helpers had assisted the breeding pairs in raising broods, the breeding pairs remained the same, and the ages of breeding birds remained within the 3- to 7-year age interval, that is, the period during which annual reproductive success remained constant for both breeding males

and females (Komdeur 1991, 1996b). Therefore, the internal control used in this study (comparing reproduction pre- and posttransfer of the same breeding pairs) is an explicit matched-pairs control for group size, age, and experience of the breeding pairs.

Weather Records

Daily weather records were kept of rainfall, maximum day temperature, and wind force. Once every 2 weeks, wind force was estimated in each territory within a 2-h period using the Beaufort scale (force 0-7). Rainfall frequency is the number of days per month (corrected to a 30-day month) that 0.1 mm or more was recorded.

RESULTS

Seasonal Food Abundance on the Islands of Cousin, Aride, and Cousine

Between May 1987 and November 1991, peak food supplies on Cousin occurred once a year between June and November. During the same period, the mean food abundance per site on Aride was on average 3.4 times higher than that on Cousin (mean $F [SD]$: 191.6 (85.7) vs. 56.2 (38.4), $n = 47$; paired-sample *t* test: $t = 13.90$, $df = 46$, $p < .001$) (Fig. 3). Minimum food abundance on Aride was almost as high as the maximum recorded for Cousin. From August 1989 to November 1991, parallel studies showed that food abundance on Cousine was on average 1.8 times higher than that on Cousin (mean $F [SD]$: 102.0 (68.9) vs. 57.6 (46.1), $n = 20$; paired-sample *t* test: $t = 5.51$, $df = 19$, $p < .001$) but 0.6 as high as that on Aride (mean $F [SD]$: 177.0 (92.1), $n = 20$; paired-sample *t* test: $t = 6.09$, $df = 19$, $p < .001$) (Fig. 3). The seasonal pattern of food abundance on Aride and Cousine was synchronous with that on Cousin (Fig. 3).

Seasonality and Timing of Breeding on Cousin

Seasonal Variation in Breeding Attempts

Breeding parameters for Seychelles warbler pairs on Cousin, the control site, are shown in Table 2. The mean number of nests built per year was 1.7, with a maximum of 5 nests. On average, courtship and nest building took 17 days. The average clutch size was 1.09. The maximum clutch laid by a single female was 2 eggs, but 91.0% of clutches were of just 1 egg. Eggs

Figure 3. Monthly food abundance ($\pm$ SE) of the islands of Aride, Cousin, and Cousine (January 1987 to November 1991).

were incubated by the females alone for an average of 18 days. Nestlings spent, on average, 19 days in the nest before fledging. The young became independent of adult feeding about 3 months after hatching.

The monthly distribution of breeding (as measured by the percentage of territories with nest-building attempts) is given in Fig. 4. Reproductive synchrony is pronounced. Between 1986 and 1991, the majority of nests were begun between May and August. Peaks of nest building ($> 60\%$ of territories with nest initiations) occurred once a year but varied between years, ranging from May to August. However, in all years, there was a second nesting season from December to February, separated from the main season by a distinct gap.

Seasonal Variation in Reproductive Success

There is a strong seasonal influence on reproductive success. The month in which nest initiations take place is of significant importance for several aspects of further reproductive success (Fig. 5 and Table 3). Compared to nest initiations starting 2 months before the food peak, nest initiations in all other months resulted in significantly lower probability of a nest containing a clutch (except when nesting occurred in the third month before insect peak) and significantly lower probability of a clutch surviving to a pullus (except when nesting occurred in the third month before insect peak), a fledgling, an independent young bird, or a yearling (Table 3). The probability of clutches producing yearlings was highest when Seychelles warblers commenced nest building 2 months prior to the insect peak, as 56.7% of such clutches resulted in the production of yearlings (Fig. 5 and Table 3). If birds started nesting and egg-laying 3 months or 1 month before the food peak, then only 3.6% or 6.1% of nesting

attempts, respectively, resulted in yearlings. When breeding commenced at the time of food peak to 8 months after the food peak, the probability of producing yearlings was only 1.1% (Fig. 5 and Table 3). Thus on Cousin, the control area, there is an overall advantage to breeding 2 months prior to the food peak. These results support the hypothesis that the timing of nest building is important when a single short food peak is present.

Proximate Cues to Reproductive Timing

Table 4 presents correlations of monthly weather variables, insect food abundance, and insect food increase with nest-building activity 2 months before to 2 months after. Weather variables considered include rainfall, rainfall frequency, temperature, and wind force. Nesting activity correlated negatively with mean maximum temperature and positively with rain frequency in the same month (Table 4). Nest-building activity was not correlated with insect food abundance in the same month but was so correlated 2 months later. However, nest-building activity was not correlated with any monthly increase in insect food (Table 4).

When variables were pooled, forward multiple regression showed that both day temperature and rain frequency had a significant overall influence on nesting activity (51.6% of total variance) (Table 5). Of these variables, day temperature explained most of the variance (43.0%). The lower the day temperature, the higher the nest-building frequency. After controlling for day temperature, rain frequency significantly affected breeding activity (Table 5). The values of remaining partial correlations were not significant.

Lower temperatures and higher rain frequency had a favorable influence on insect abundance 2 months later (Table 6). Most young warblers were present at the peak time of insect abundance (Table 6). Two months not only was the time lag between the influence of temperature or rain frequency on insect food availability, it was also the time needed for courtship/nest building, incubation, and hatching (Table 2). Therefore, by responding to a decrease in day temperature and an increase in rain frequency, the warblers timed their nest building such that insect food was at a maximum when it was most needed: 2 weeks after hatching, when nestling growth is maximal (Komdeur, 1991). It seems that warblers show a flexibility in the initiation of breeding. During the 5-year study period on Cousin, each year warblers shifted the onset of breeding in accordance with the food peak about 2 months later (Fig. 6).

Table 2. Breeding parameters ($\pm$ SD) of unassisted Seychelles warbler pairs on Cousin Island over a 5-year period (1986 to 1990).

Productivity	Mean	SD	Range	n
Yearly nesting attempts	1.67	0.99	0-5	289
Days courtship/nest building	17.2	0.85	7-29	42
Clutch size	1.09	0.34	1-2	223
Days incubation	18.0	0.53	17-19	41
Days fledging	19.2	0.60	18-20	63
Days to independence	88.5	19.71	70-240	189

NOTE: n = territory-years.

Figure 4. Percentages of territories with nest attempts each month on the islands of Cousin (January 1986 to November 1991), Aride (October 1988 to November 1991), and Cousine (July 1990 to November 1991). Mean nesting activities on Aride and Cousin (October 1988 to November 1991) are 96.7% (mean $n = 21$) and 15.8% (mean $n = 82$), respectively. Mean nesting activities on Aride, Cousin, and Cousine (July 1990 to November 1991) are 98.4% (mean $n = 19$), 16.8% (mean $n = 38$), and 33.8% (mean $n = 12$), respectively.

Interisland Comparison of Breeding Activity Following the Transfers

The transferred birds swiftly accepted their new habitats on Aride and Cousine, formed pairs with their original mates or with new mates, and began establishing territories within days—and in some cases hours—of being released. At the beginning of October 1988, after 2 weeks, 13 territories were established on Aride; of these, 11 were occupied by pairs and 2 by single males. The other 5 birds have been seen wandering over the island on their own. At the beginning of July 1990, after 1 week, 12 territories were established on Cousine; of these, 8 were occupied by pairs and 4 by single males. The other 9 birds were

Figure 5. Mean monthly reproductive performances by Seychelles warbler pairs on the islands of Cousin (January 1987 to September 1990) and Aride (September 1988 to September 1990) before, at the time of (Month 0), and after the annual food peak. Percentages of nest-building attempts resulting in clutches (top numbers are numbers of nest-building attempts) and percentages of clutches resulting in the production of nestlings, fledglings, independent young birds, and yearlings (top numbers are numbers of clutches) are shown.

seen wandering over the island on their own. The most striking aspect of both transfers was the burst of nesting activity by birds immediately following release and that breeding on Aride occurred outside the "normal" breeding period on Cousin. On both islands, successful nesting started in most territories within a few weeks, and in some territories within 3 days, of release. The first young birds on Aride (twins) and Cousine were hatched by experienced breeders 4 and 3 weeks after the transfer, respectively.

Comparing the percentages of territories with nest-building activity on Aride and Cousin for the 3 years and 2 months after the transfer (Fig. 4), Aride birds showed, on average, 6.1 times more nest-building ac-

Table 3. Mean reproductive performance by Seychelles warbler pairs on the islands of Cousin (January 1987 to September 1990) and Aride (September 1988 to September 1990) during the second month before the insect food peak compared to reproductive performance in other periods.

	Months between Nest-Building Activity and Insect Food Peak				
	-7/-4	-3	-2	-1	0/+4
Cousin					
Percentage nests with clutches	38.5**	75.7	94.4	54.1**	57.5**
<i>n</i>	104	37	71	61	94
Percentage clutches producing nestlings	35.0**	78.6	89.6	63.6*	40.7**
Percentage clutches producing fledglings	20.0**	50.0**	80.6	30.3**	22.2**
Percentage clutches producing independent young birds	2.5**	21.4**	68.7	15.2**	11.1**
Percentage nests producing yearlings	0.0**	3.6**	56.7	6.1**	1.9**
<i>n</i>	40	28	67	33	54
Aride					
Percentage nests with clutches	100.0	100.0	100.0	100.0	87.9
<i>n</i>	33	10	10	9	33
Percentage clutches producing nestlings	78.8	60.0	70.0	100.0	89.7
Percentage clutches producing fledglings	69.7	60.0	50.0	88.9	79.3
Percentage clutches producing independent young birds	69.7	60.0	50.0	88.9	79.3
Percentage clutches producing yearlings	69.7	60.0	50.0	88.9	79.3
<i>n</i>	33	10	10	9	29

NOTE: *n* = number of nest attempts. Statistical significance of comparisons was determined by one-tailed χ^2 contingency analysis.

p* < .01; *p* < .001.

Table 4. Spearman rank correlations of monthly weather variables, insect food abundance, and insect food increase with monthly nest attempts by Seychelles warbler pairs 2 months before to 2 months after on the islands of Cousin (*n* = 41, May 1987 to September 1990) and Aride (*n* = 24, October 1988 to September 1990).

	Months between Environmental Factor and Nest Attempts				
	-2	-1	0	+1	+2
Cousin					
Weather variables					
Rainfall	-.18	-.15	-.02	.14	.02
Rainfall frequency	-.27	-.04	.40*	.21	.17
Temperature	-.15	-.53**	-.66**	.28	.20
Wind force	.03	.23	.31	.30	.10
Insect food abundance	.62**	.29	.22	-.16	-.04
Insect food increase	.21	.04	.14	-.13	.03
Aride					
Weather variables					
Rainfall	-.08	-.12	.06	.15	-.13
Rainfall frequency	-.13	-.06	.13	-.16	.13
Temperature	.03	-.13	.12	.11	.01
Wind force	.03	.12	-.11	.02	-.16
Insect food abundance	-.11	.23	.09	.12	.05
Insect food increase	.13	.12	.09	.08	-.04

p* < .05; *p* < .001.

tivity than did Cousin birds (paired-sample *t* test: *t* = 23.92, *df* = 37, *p* < .001). The seasonal pattern in the percentage of territories with nesting activity on Aride was not synchronous with that on Cousin in the same month. A minimum of 64% of pairs bred on Aride in October 1988, and a maximum of 90% to 100% of pairs

were breeding from January 1989 to November 1991. Over the same period, the percentage of breeding pairs on Cousin varied from 0% (October and November 1988 and June 1989) to 96% (August 1991 only). Nest-building activity by warblers on Aride was not correlated with any weather variables, with insect food abundance, or

Table 5. Combined effects of weather variables, insect food abundance, and insect food increase on nest-building activity by Seychelles warbler pairs on Cousin Island (forward multiple regression, $n = 41$ observations, May 1987 to September 1990).

Independent Variable	Cumulative r^2	P
Day temperature	.430	< .001
Rainfall frequency	.516	< .001
Rainfall	.524	.618
Wind force	.526	.820
Insect food abundance	.530	.725
Insect food increase	.532	.657

with insect food increase (Table 4). It seems that the timing of nest building on Aride was not important for nesting success, which was the same for any given month or period and significantly higher than nesting success on Cousin (Fig. 5 and Table 3).

Comparing the percentages of territories with nest-building activity on the three islands for 1 year and 5 months following the transfer to Cousine (Fig. 4), Cousine birds showed, on average, 2.9 times more nest-building activity as did Cousin birds ($t = 2.92$, $df = 16$, $p < .01$) but 2.9 times less than did Aride birds ($t = 12.86$, $df = 16$, $p < .001$). There appeared to be one annual peak of breeding activity in the populations on Cousin (June/July) and Cousine (August). The seasonal pattern in the percentage of territories with breeding activity on Cousine was synchronous with that on Cousin in the same month but not with that on Aride.

Intraindividual Comparison of Breeding Activity Before and After Transfer

During the 2-year period before transfer, experimental and control units had the same annual production of fledglings and yearlings (Fig. 7). After transfer of the experimental groups to the islands of Aride and Cousine, reproductive success of these groups increased significantly. At the same time, reproductive success of control groups remaining on Cousin and obeying the same selective criteria did not change significantly (Fig. 7).

Over the 2-year period following the transfer to Aride, the production of yearlings per experimental pairs on this island was significantly higher than that by the same pair on Cousin during the 2-year period before the transfer (Table 7). The increase in reproduction can be attributed to three factors: (1) higher number of nesting attempts per pair (on average, 3.5 times as many as on Cousin); (2) higher survival of clutches to hatching (1.6 times) and, consequently, higher number of nests with pulli (5.9 times) and nests producing

fledglings (6.6 times); and (3) higher survival of fledglings to 1 year of age (3.5 times) and, consequently, higher number of 1-year-old young produced per pair. Taken together, the production of yearlings per experimental pair was, on average, 23.0 times higher on Aride. The increase in reproduction was due not only to more breeding attempts per year but also to a higher nesting success (Table 7). This can be attributed to a larger clutch size (1.8 times) and, as a consequence, more nestlings per nest (2.4 times), higher nestling survival to fledging (1.8 times), more fledglings per nest (2.7 times), and higher fledgling survival to 1 year of age (1.6 times). Given that mean territory quality of experimental pairs on Aride was 15.9 times higher than that on Cousin (Table 7), it is no wonder that Aride birds were able to sustain high breeding output.

The production of offspring per experimental pair on Cousine in the 1-year following the transfer was significantly higher than that by the same pair on Cousin (Table 7). This was due mainly to the higher number of nests built per territory (2.3 times), not (as on Aride) to higher nesting success. Percentage of nests with clutch, clutch size, hatching, and fledging success were all slightly, but not significantly, higher on Cousine. In addition, fledgling survival to 1 year of age was 5 times higher on Cousine. Taken together, these factors resulted in a 5 times higher production of yearlings by the experimental pairs. Mean territory quality of experimental pairs on Cousine was 3.4 times higher than that on Cousin (Table 7). These results are in agreement with the fact that the quality of warbler territories was intermediate compared to that of Aride and Cousin (Table 7).

Increased breeding on Aride and Cousine is not caused because temperature and rain levels are above a certain threshold level during part or all of the year. Mean monthly temperature, monthly rainfall, and monthly rainfall frequency on these islands (Table 7), as well as their annual patterns (Komdeur, 1994a, 1996a), were the same as those on Cousin (Table 7).

DISCUSSION

Window for Successful Reproduction on Cousin Island

Among Seychelles warblers on Cousin, close to the equator, reproduction is seasonal, as it is in temperate zone birds. The seasonal time schedule is rather tight: the onset of breeding during the main breeding season varied by only 4 months between years. However, in

Table 6. Spearman rank correlations of monthly weather variables and reproductive success by Seychelles warbler pairs with monthly insect food abundance on Cousin Island ($n = 41$, 2 months before to 2 months after, May 1987 to September 1990).

	Months between Change in Variables and Insect Food Abundance				
	-2	-1	0	+1	+2
Weather variables					
Rainfall	-.13	-.29	.00	-.17	-.17
Rainfall frequency	-.02	.24	.27	.12	.46*
Temperature	.02	-.20	-.21	.02	-.53**
Wind force	.23	-.03	.06	.17	.29
Reproductive success					
Nest building	.04	-.16	-.22	.30	.62**
Nestlings	.18	.04	.78**	.34	.21

* $p < .002$; ** $p < .001$. Figure 6. Correlations between months of maximum food abundance and months with highest percentages of nest initiations, measured yearly, from 1987 to 1991 ($r = .95$, $n = 5$, $p < .025$).

all years, there was a smaller, second nesting season from December to February, separated from the main season by a distinct gap. This second nesting peak was due to the presence of warbler pairs breeding on the small southeastern part of the island (6 hectares) protected by the hill. During the northwest monsoon season from December to March, this sheltered area was significantly less defoliated and had higher insect food abundance than did the northwest half of the island (Komdeur, 1996c). The results of the present study suggest that the variability in abundance of insect food may contribute to the observed natural variation in the onset of breeding in Seychelles war-

Figure 7. Annual numbers of yearlings produced per experimental (open bars) and control (shaded bars) pairs of Seychelles warblers 2 years before (Aride: 1986 to 1988; Cousine: 1988 to 1990) and 2 years (1988 to 1990) or 1 year (1990 to 1991) after the transfer to the islands of (A) Aride in 1988 and (B) Cousine in 1990. Means, standard deviations, and sample sizes are shown. p values for differences between experimental and control groups were determined by one-tailed Mann-Whitney U test; those for pre- and postremoval were determined by one-tailed paired-sample t test. NS denotes $p > .05$.

blers. Insect food was abundantly available during only 1 or 2 months per year. My results support current

Table 7. Comparison of mean annual breeding performance and mean monthly territory quality of 5 Seychelles warbler pairs and mean monthly weather variables ($\pm$ SD) on Cousin Island before (October 1986 to September 1988) and on Aride Island after translocation (October 1988 to September 1990), and of 4 pairs on Cousin before (July 1988 to June 1990) and on Cousine Island after translocation (July 1990 to June 1991).

	Experimental Groups (n = 5)			Experimental Groups (n = 4)		
	Cousin (1986-1988)	Aride (1988-1990)	p	Cousin (1988-1990)	Cousine (1990-1991)	p
Annual performance/pair						
Nest attempts	1.50 $\pm$ 0.50	5.20 $\pm$ 0.45	< .001	1.00 $\pm$ 0.82	2.25 $\pm$ 1.26	< .025
Percentage nests with clutches	90.0	94.4	n.s.	75.0	81.3	n.s.
Nests with clutches	1.30 $\pm$ 0.27	4.90 $\pm$ 0.42	< .001	1.00 $\pm$ 0.71	1.75 $\pm$ 0.96	< .025
Percentage clutches hatched	63.3	96.0	< .05	50.0	79.2	n.s.
Nests with pulli	0.80 $\pm$ 0.45	4.70 $\pm$ 0.45	< .001	0.50 $\pm$ 0.41	1.25 $\pm$ 0.50	< .025
Percentage nestlings fledged	80.0	97.8	n.s.	50.0	100.0	n.s.
Nests producing fledglings	0.70 $\pm$ 0.57	4.60 $\pm$ 0.55	< .001	0.38 $\pm$ 0.48	1.25 $\pm$ 0.25	< 0.01
Percentage fledglings reaching 1 year of age	16.7	100.0	< .01	12.5	100.0	< .05
Nests producing yearlings	0.20 $\pm$ 0.27	4.60 $\pm$ 0.55	< .001	0.13 $\pm$ 0.25	1.25 $\pm$ 0.50	< .01
Fate of clutch						
Clutch size	1.00 $\pm$ 0.00 (13)	1.76 $\pm$ 0.57 (45)	< .001	1.00 $\pm$ 0.00 (6)	1.14 $\pm$ 0.35 (7)	n.s.
Percentage eggs hatched	84.6 (13)	95.6 (79)	n.s.			
Nestlings hatched/nest	0.62 $\pm$ 0.51 (13)	1.51 $\pm$ 0.66 (45)	< .01			
Percentage nestlings fledged	54.6 (11)	97.1 (68)	< .005			
Nestlings fledged/nest	0.54 $\pm$ 0.52 (13)	1.47 $\pm$ 0.63 (45)	< .02			
Percentage fledglings reaching 1 year of age	63.6 (7)	100.0 (66)	< .005			
Yearlings produced/nest	0.15 $\pm$ 0.38	1.47 $\pm$ 0.63 (45)	< .001			
Mean territory quality	15.5 $\pm$ 10.3	246.6 $\pm$ 46.3	< .001	8.5 $\pm$ 6.0	28.9 $\pm$ 7.4	< .025
Mean monthly temperature ($^{\circ}$ C)	30.2 $\pm$ 1.4	30.5 $\pm$ 1.8	n.s.	30.8 $\pm$ 1.2	30.5 $\pm$ 1.4	n.s.
Main monthly rainfall (mm)	140.2 $\pm$ 60.1	121.8 $\pm$ 98.2	n.s.	132.4 $\pm$ 57.2	135.2 $\pm$ 45.9	n.s.
Main monthly rainfall frequency (days)	13.1 $\pm$ 2.3	15.2 $\pm$ 2.4	n.s.	16.8 $\pm$ 3.1	17.5 $\pm$ 2.9	n.s.

NOTE: Numbers of observations are in parentheses. Statistical significance of breeding performance comparisons was determined by one-tailed paired-sample *t* test and one-tailed Wilcoxon test (percentage data). Statistical significance of other comparisons was determined by one-tailed *t* test (fate of clutch), two-tailed *t* test (environmental data), and χ^2 contingency analysis (percentage data). n.s. = *p* > .05.

theory on timing of breeding seasons (Lack, 1966; Perrins, 1970; Robertson, 1973): increased failure of nest-building attempts late in the season may cause females to breed as early as possible. The percentage of nest-building attempts resulting in the production of yearlings was highest (53.5%, *n* = 67) when warblers commenced nest building 2 months prior the insect peak. Two months was also the time needed for courtship, nest building, incubation, and hatching. If these birds started earlier or later, only 2.6% of nest initiations (*n* = 155) resulted in the production of yearlings. This was due to a lower probability of a nest containing a clutch or lower survival of the clutch to a yearling. It seems that if the birds hatch their eggs too early or too late, then food supply is not high enough to satisfy the needs of the nestlings and fledglings. As a consequence, fledging success and the probability of reaching independence were significantly lower.

To begin breeding, females may require a certain minimal amount of food as an indicator of availability of food in the future when young need to be fed. Lower temperature and higher rain frequency had a favorable influence on insect abundance 2 months later. Both factors affect food availability through their ef-

fects on plant and insect phenology (Komdeur, 1991). On Cousin, warblers seem to use a decrease in day temperature and/or an increase in rain frequency as cues in their breeding decisions rather than a change in rate of increase in insect food availability. In so doing, they time their nest building such that the presence of nestlings is synchronized with peak abundance of food. Food was at a maximum when it was most needed: 2 weeks after hatching, when nestling growth is maximal (Komdeur, 1991). There apparently is continuous selection for correct timing of breeding on Cousin (a narrow window for successful reproduction). My observational results suggest that the reproductive performance of Seychelles warblers was independent of breeding density; the number of territories and number of birds on the island remained the same at the time of study.

The data for Cousin are not conclusive evidence that the onset of breeding is constrained because females may obtain insufficient nutrients for the manufacture of eggs (Perrins, 1970); in some months with low food availability and low nesting success, the probability of producing an egg was the same as that in months with high food availability and high nesting success (Fig. 5).

Food Limitation Hypotheses for Reproductive Timing and Success

Ewald and Rohwer (1982) have argued that if individuals of a species can predict future food supply, then selection may favor flexibility in the initiation of breeding such as red-winged blackbirds (*Agelaius phoeniceus*) (Ewald and Rohwer, 1982), European kestrels (*Falco tinnunculus*) (Drent and Daan, 1980), and song sparrows (*Melospiza melodia*) (Smith et al., 1980). If not, selection may act against flexibility, as in crows (*Corvus corone*) (Yom-Tov, 1974), tits (willow tit [*Parus montanus*] and crested tit [*Parus cristatus*]) (Brömssen and Jansson, 1980), and magpies (*Pica pica*) (Högestedt, 1981). My data on the onset of breeding in Seychelles warblers on Cousin suggest that the birds are flexible in the initiation of breeding: warblers timed their breeding so that insect food was at a maximum when the nestlings hatched, and they shifted the onset of breeding in accordance to insect food peaks.

The transfers of Seychelles warbler breeding pairs to unoccupied islands with the same vegetation and climatical conditions as Cousin but with significantly more insect food available confirmed the plasticity in breeding. On the new islands, reproductive success of the warblers was significantly higher. The resulting degrees of advancement and increase in breeding are correlated with the levels of food abundance on the new islands. These results were controlled for group size, age, and breeder experience.

It is clear that the differences in reproductive timing and the number of offspring produced by warblers on the three islands are due not to genetic differences but entirely to differences in environmental conditions. On Aride and Cousine, with the same vegetation (Komdeur, 1994a) and climatical conditions, the abundance of insect food appears to be a crucial factor. Unlike nesting activity of warblers on Cousin, which is correlated negatively with day temperature and positively with rainfall frequency in the same month, nesting activity of birds on Aride is not correlated with any weather variables. On Aride, there is no need to time nesting activity, because offspring survival is high and constant throughout the year. However, in nearly all other studies, food-supplemented females started laying by only a few days up to 1 week earlier than did control females (see Meijer et al., 1990, Table 1), suggesting that cues other than food abundance are important. Meijer et al. (1990) and Schultz (1991) suggested that there exists a "reproductive window" dur-

ing which breeding can take place and also envisage a linear relationship between food abundance and start of laying. However, despite the existence of a narrow window for successful reproduction on Cousin, breeding on the new islands also takes place successfully outside this window: on Aride, birds bred the whole year-round. It seems that reproduction on Aride was not constrained by molt; birds were able to molt and breed at the same time (Komdeur, 1996a). On Cousin, however, birds undergo a prebreeding molt; of all the possible monthly molting and breeding activity combinations, the only significant correlation found was between the percentage of territories with nests and the percentage of molting birds 2 months earlier ($r = .68$, $df = 52$, $p < .001$) (Komdeur, 1996a).

Schultz (1991) argued that there exists a "saturation" (i.e., threshold) level of energy below which breeding cannot start. Above this level, however, breeding date is unrelated to nutritional state, and breeding is initiated in response to some environmental cue(s) correlating with parental fitness. This hypothesis, which agrees with Perrins' (1970) original idea, would explain why food provision experiments in temperate zone birds usually have advanced laying by only a few days up to 1 week. However, tropical bird species may show a higher response to increased food availability. Apparently, birds on Aride base their decisions of when to start laying entirely on their own nutritional states. Adult warblers on Aride were, on average, significantly heavier than adult warblers on Cousin (mean male weight [grams (SD)], Aride vs. Cousin: 17.3 (0.22) vs. 16.4 (0.80), $t = 4.33$, $df = 123$, $p < .001$; mean female weight [grams (SD)]: 15.8 (0.52) vs. 14.7 (0.74), $t = 5.64$, $df = 91$, $p < .001$). It seems that warblers on Aride are in a much better condition and possibly above the threshold energy level for breeding. In this case, there is no need to use cues other than insect food abundance for timing of breeding. It may be that the threshold level for breeding in the Seychelles warbler is linked with the amount of hormones in the blood and the development of gonads. By determining the amount of hormones in the blood and scoring gonad development in live birds with the laparotomy technique (Dittami and Gwinner, 1985), it is possible to check for circannual patterns in hormones and gonad development. Without gonad data, it is not possible to make definitive statements, but the fact that birds are capable of breeding year-round and are seasonal suggests that they may be able to show responses to a wide variety of stimuli. I would expect that birds on Cousin

respond to increases in food with gonadal growth and have well-developed gonads during insect food peaks and that birds on Aride have well-developed gonads year-round because of continuous high food availability.

Social Disruption Hypothesis for Reproductive Success

Tompa (1964) suggested that high population density caused sufficient social disruption and stress in breeders to depress reproduction. My study was not designed to test this hypothesis, but there are two indications that high levels of territorial aggression cannot explain the differences in reproductive performance of experimental pairs. First, both on Cousin and on the new islands, the territories of experimental pairs were equally surrounded by territories. Second, on the new islands, the intrusion pressure by nonterritorial males into experimental territories was more frequent than it was on Cousin because of high competition for females (Komdeur, unpublished results).

Effect of Additional Food on Clutch Size

In most previous studies that provided supplemental food to passerine birds, fed individuals advanced the timing of egg laying, often by as much as 3 weeks, but did not lay larger clutches (reviewed in Arcese and Smith, 1988; Boutin, 1990; Rohwer, 1992). Of 14 food supplementation studies reviewed by Arcese and Smith (1988), only 5 (36%) reported increases in clutch size. Davies and Lundberg (1985) suggested that larger species might respond more readily to supplemental food because the formation of eggs limits their reproductive output (Winkler, 1985). Smaller species, on the other hand, may be limited more by the ability of the parents to feed their young. My results are contrary to this hypothesis. On Aride, with significantly more food available per territory than on Cousin, I observed a twofold increase in clutch size among Seychelles warblers, a species in which females weigh about 14.7 g. This is in agreement with the study by Arcese and Smith (1988), in which fed song sparrows, a species in which females weigh about 23 g, increased their clutch sizes.

Safriel (1972) suggested that clutch size in nidifugous birds is limited by the ability of the parents to protect their young from predation. However, this suggestion does not explain the determination of clutch size in the Seychelles warbler. Despite the same

predator species and same predation pressure on the islands (Komdeur, 1994a, 1996a), most females on Aride laid 2 eggs per clutch compared to 1 egg by the same females on Cousin. In one case, a clutch laid by 1 female consisted of 4 eggs and survived to produce 4 fledglings, of which 3 became yearlings. Also, hatching and fledging success on Aride was significantly higher.

Dijkstra et al. (1982) found that European kestrels increased their clutch sizes in response to supplemental food, but only to the extent predicted by an observed negative relationship between clutch size and laying date. In the Seychelles warbler population, however, I would not expect such a result because clutch size is nearly always 1, independent of laying date (Komdeur, 1991).

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