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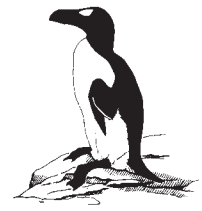
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RAPID COMMUNICATIONS

EXPERIMENTAL REINTRODUCTION REVEALS NOVEL LIFE-HISTORY VARIATION IN LAYSAN DUCKS (*ANAS LAYSANENSIS*)

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ABSTRACT.—Subfossil remains indicate that the Laysan Duck (*Anas laysanensis*) formerly occurred throughout the Hawaiian archipelago, but for more than 150 years it has been confined to a single, small atoll in the northwestern chain, Laysan Island. In 2004–2005, 42 ducks were reintroduced from Laysan to Midway Atoll, where they exhibited variation in life history never observed on Laysan. On Laysan, females have never been observed to breed successfully at age 1 year and few attempt it, whereas on Midway, females routinely raised young at <1 year of age. Mean (\pm SD) clutch size on Midway (7.0 ± 1.1 , $n = 41$) was larger than the maximum clutch size of six eggs observed on Laysan. On Midway, renesting following nest failure (0.55 probability, $n = 27$) and double brooding (0.50, $n = 54$) were routine, and two instances of triple brooding were observed, whereas on Laysan, renesting and double brooding are rare (0.05 probability for both during our study; $n = 21$ and 19, respectively) and triple brooding has never been observed. Other novel life history on Midway included early cessation of parental care to renest. Altered life history on Midway is likely related to better feeding conditions and low population density compared with Laysan. An especially intriguing possibility is that the phenotypic plasticity observed represents exposure of hidden reaction norms evolved when the species inhabited a range of environments, but several alternative explanations exist. Future reintroductions of this species may provide opportunities to test hypotheses about mechanisms underlying phenotypic plasticity. Received 24 April 2013, accepted 16 July 2013.

Key words: *Anas laysanensis*, clutch size, endangered species, Hawaii, Laysan Teal, life history, phenotypic plasticity, reintroduction.

La Reintroducción Experimental Revela Nueva Variación sobre la Historia de Vida de *Anas laysanensis*

RESUMEN.—Los restos subfósiles indican que *Anas laysanensis* antiguamente se encontraba en todo el archipiélago hawaiano, pero por más de 150 años la especie ha estado confinada a un único y pequeño atolón en la cadena noroccidental, la isla Laysan. Entre 2004 y 2005, se reintrodujeron 42 patos de la isla Laysan en el atolón Midway, donde exhibieron variación en su historia de vida que no había sido observada en Laysan. En Laysan, nunca se había observado que las hembras se reprodujeran exitosamente en su primer año y pocas lo intentan, mientras que en Midway, las hembras rutinariamente criaban polluelos siendo menores que 1 año de edad. El tamaño de nidada promedio (\pm DE) en Midway (7.0 ± 1.1 , $n = 41$) fue mayor que el tamaño máximo de nidada ($n = 6$) observado alguna vez en Laysan. En Midway, la frecuencia de reanidación luego del fracaso de nidos (probabilidad 0.55, $n = 27$) y la anidación doble (0.50, $n = 54$) fueron rutinarias y se observaron dos situaciones de anidamiento triple. En Laysan la reanidación y la anidación doble son raras (probabilidad de 0.05 para ambos durante nuestro estudio, $n = 21$ y 19, respectivamente) y nunca se ha observado anidación triple. Otras novedades de la historia de vida en Midway incluyen la terminación temprana del cuidado parental para volver a anidar. La historia de vida alterada en Midway probablemente esté relacionada con mejores condiciones de alimentación y bajas densidades poblacionales en comparación

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con Laysan. Una posibilidad espacialmente intrigante es que la plasticidad fenotípica observada representa la exposición de normas de reacción ocultas que evolucionaron cuando la especie ocupaba un mayor rango de condiciones ambientales, pero existen muchas explicaciones alternativas. Las reintroducciones futuras de esta especie podrían proveer oportunidades de probar hipótesis sobre los mecanismos responsables de la plasticidad fenotípica.

PHENOTYPIC PLASTICITY is the production of different phenotypes from a common genotype in response to different environments.¹ Here, we describe unexpected life history traits in the endangered Laysan Duck (*Anas laysanensis*) following a shift in environments resulting from a wild-to-wild reintroduction. Because of the history of this species, these observations are especially relevant to possible mechanisms underlying phenotypic plasticity and the role of phenotypic plasticity in adaptive evolution.^{1,2}

HISTORY AND BIOLOGY OF LAYSAN DUCKS

The Laysan Duck is a formerly widespread Hawaiian species that inhabited diverse environments, but in recent times it has been confined to a small, low-lying atoll. Subfossil remains of Laysan Ducks are widespread and indicate that the species once occurred throughout the Hawaiian archipelago.^{3,4,5} The species is apparently an insectivorous habitat generalist, once occurring from high-altitude forests to coastal wetlands,^{4,5} but, like many other Hawaiian birds,³ it was extirpated from the large islands following the arrival of humans and introduced rats 800–900 years ago.⁶ Unlike most of these species, the Laysan Duck survived on small islands in the remote northwestern chain, inhabiting Lisianski Island, from which it was extirpated in the mid-1800s,⁷ and Laysan Island, where it persists (Fig. 1).

Laysan is an atoll with 147 ha of mostly low herbaceous vegetation; 152 ha of unvegetated blowout areas, coastal dune, and beach; and 74 ha of interior hypersaline lake and associated mudflats.⁸ Laysan Ducks declined to near extinction between 1905 and 1925, following the intentional introduction of European Rabbits (*Oryctolagus cuniculus*) to Laysan,⁹ which almost completely destroyed the island's vegetation. Three of the island's five endemic land birds went extinct during that period,¹⁰ and at one point only seven Laysan Ducks, including a single female, could be found on the island. The actual number of survivors was likely higher, but clearly the species was reduced to only a handful of pairs at best.⁹ The population recovered to 400–600 birds, though it has fluctuated in size and in 1993–1994 fell to only ~150 adults during a severe drought.^{11,12}

The Laysan Duck is well studied, and its life history on Laysan Island has been documented repeatedly over an extended period.^{10,11,13,14} The Laysan Duck is characterized by low reproductive effort compared with congeneric species. Clutch size is small, and eggs are large in relation to body size.¹⁵ Males and females form pair bonds: pairs remain together through early incubation, females usually reunite with their mates if broods fail early in the breeding season, and mate fidelity between years is high.^{10,11,16} Renesting after nest failure is uncommon. Females attend ducklings until they are 45–75 days old, and as a result successful double brooding is extremely rare, having been recorded only twice.¹⁷ Females may delay breeding for several years, and known-age females have never been observed breeding successfully at 1 year of age. Annual variation in productivity is due largely to breeding propensity, with only a few females attempting to breed in some

years, and duckling mortality¹⁷; complete reproductive failure has occurred occasionally.^{10,11} These fluctuations appear to be tied to rainfall and the abundance of a food critical to reproduction, brine flies (*Scatella sexnotata*),^{11,17} as well as to population density.¹⁸ Even during productive years and when population density is low, clutch sizes and individual nesting effort remain small.^{11,17,18} Annual survival of adults (females: 0.88, males: 0.91)¹⁹ and fledged juveniles (0.82)¹³ is high and unrelated to population density.¹³

REINTRODUCTION TO MIDWAY AND DATA COLLECTION

To reduce the risk of extinction inherent to a species confined to a single small island vulnerable to catastrophes such as cyclones and tsunamis, wild Laysan Ducks were moved to Midway Atoll²⁰ to establish a second population on another island in the northwestern chain. Midway is within the Papahānaumokuākea Marine National Monument and is 600 km from Laysan (Fig. 1). Twenty wild Laysan Ducks were translocated to Midway in October 2004, and another 22 were moved in October 2005. Of these, 32 were 2.5 to 5 months of age, four were 14 to 18 months, two were ≥14 months, and two were ≥24 months.²⁰ Midway is larger (597 ha of land area) than Laysan; has much greater habitat diversity, albeit most of it in the form of non-native vegetation; and contains 2.2 ha of freshwater wetlands enhanced or created by humans.²¹ Midway also has greater invertebrate diversity than Laysan, again mostly in the form of introduced species.²² The combination of low population density and a relatively rich (compared to Laysan) environment likely resulted in favorable conditions for the ducks.

Translocation of ducks to Midway and postrelease monitoring are described in detail here.^{20,23} Briefly, all founders were given unique color-band combinations and custom-designed and -fitted radiotransmitters (Advanced Telemetry Systems, Isanti, Minnesota, and AVM Instrument, Colfax, California) attached with quick-release back-pack harnesses (Sirtrack, Havelock North, New Zealand). Bird locations were determined both day and night, one to six times per week depending on the bird's breeding status. Handheld antennas were used for homing on transmitter signals, which enabled us to monitor movements and initiation of incubation and record the outcome of nearly all nesting attempts. All ducklings were color banded at 20–60 days of age and fitted with radiotransmitters at 60–90 days of age during 2005 and 2006. In 2007, we monitored a sample of females on Midway using radiotransmitters and obtained additional data from females without transmitters by checking all wetlands daily for the arrival of new broods. Broods are typically brought to fresh water within a few days of hatching,¹¹ and because all adult females were uniquely marked, each new brood could be associated with an individual female.

Comparisons to Midway are based on data collected on Laysan by the same methods and during approximately the same period. Quantitative comparisons are limited to data collected on Laysan during 1999–2000 and 2004–2007 from females with

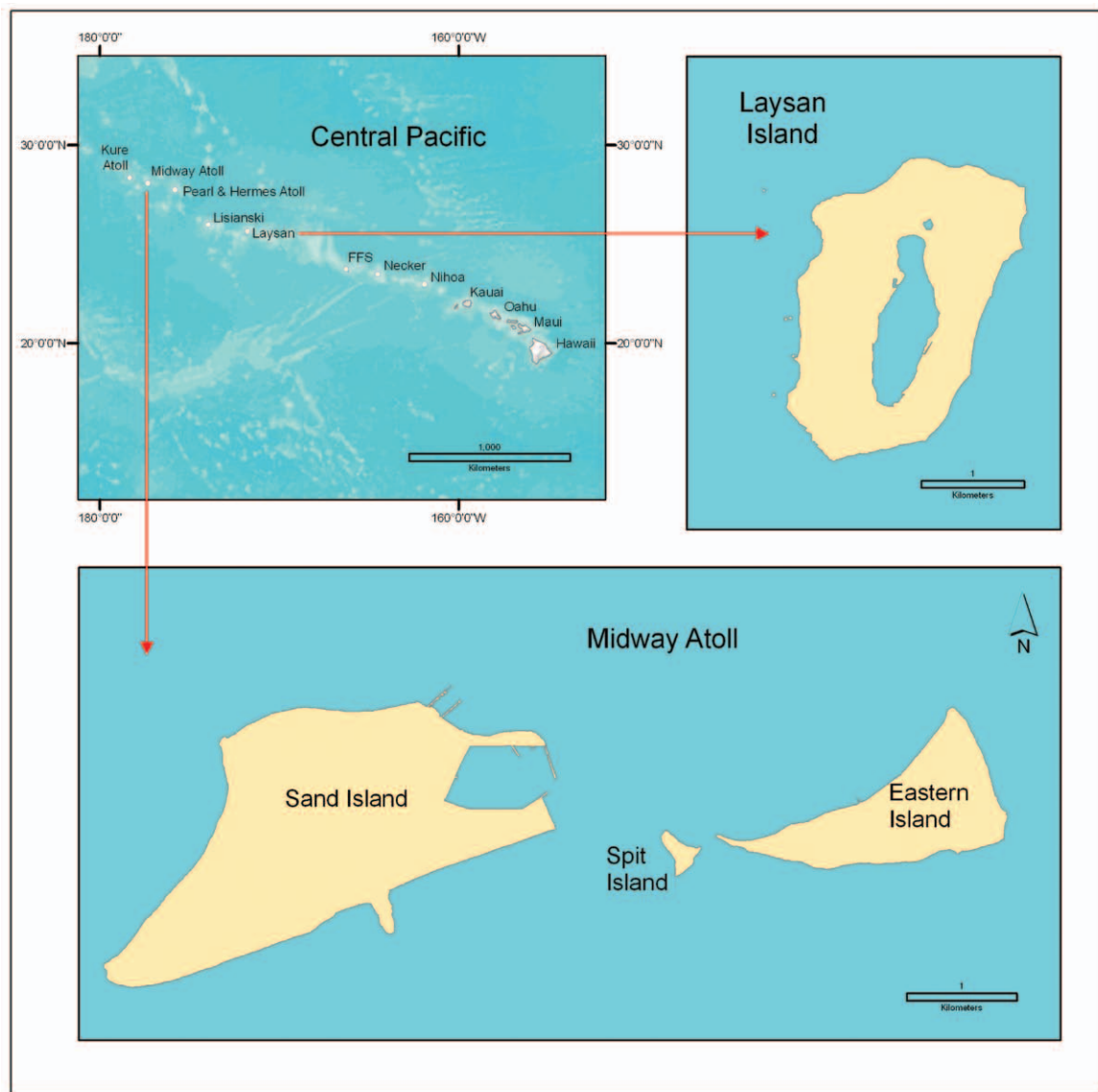


FIG. 1. Map of Hawaiian Islands with enlargements of Laysan Island and Midway Atoll.

identical radiotransmitters and attachment methods as employed on Midway. Locations were obtained 2–5 times week⁻¹ from a sample of females (7–25 females year⁻¹) each year, and all nesting attempts of these females were monitored. (For additional details on data collection methods on Laysan, see here^{17,24}). Additional qualitative data were obtained from females without transmitters by checking daily for broods around the central lake during the breeding seasons of 1998–2000 and 2003–2007. On Laysan, females bring their broods to freshwater seeps along the margins of the lake within a few days of hatching.¹¹

DIFFERENCES IN LIFE HISTORY ON MIDWAY AND LAYSAN

Values of life history traits recorded on Laysan during our study were similar to those reported in previous studies.^{10,11,13,14} By contrast, the values recorded on Midway in many cases were well

beyond the range of values observed on Laysan in this or previous studies (Table 1). Birds began to breed within 6 months of being translocated to Midway, most females bred every year, and 12 females were documented nesting successfully at ≤ 1 year of age. No females were observed breeding successfully at age 1 year on Laysan during the study. Clutch sizes of first nests on Midway were significantly larger than those on Laysan ($t = 3.65$, $P < 0.001$) (Table 1). In fact, the average clutch size for first nests on Midway was larger than the maximum clutch size observed on Laysan during this or previous studies, and the mean on Laysan was smaller than the minimum observed on Midway (Fig. 2). Clutch sizes declined with clutch number on Midway, but not dramatically so, from 7.0 ± 1.1 ($n = 41$, range: 4–10; means are presented \pm SD throughout) for first clutches to 6.3 ± 1.5 ($n = 28$, range: 2–8) for second clutches to 6.1 ± 1.6 ($n = 14$, range: 2–8) for clutches 3 to 5 (analysis of variance, $F = 2.92$, $P = 0.06$).

TABLE 1. Life history traits of Laysan Ducks on Laysan Island and Midway Atoll. Statistics are reported as means, with sample size in parentheses. Data are from radiotagged birds only unless marked by an asterisk. Clutch size is for first nests only (mean \pm SD). P_{nesting} is the annual probability of nesting, “re nesting” is the probability of re nesting after nest failure (all nesting attempts included), “double brooding” is the probability of initiating a new nest after a successful nest (all nesting attempts included), “ ≥ 3 attempts” is the proportion of females attempting three or more nests in the same year, and “age first brood” is the minimum age at first breeding.

Trait	Laysan	Midway
Clutch size	3.3 \pm 1.4 eggs (33)	7.0 \pm 1.1 eggs (41)
P_{nesting} ^a	0.44 (54)	0.95 (43)
Renesting ^a	0.05 (21)	0.55 (27)
Double brooding ^a	0.05 (19)	0.50 (54)
≥ 3 attempts ^a	0 (41)	0.24 (41)
Age first brood*	2 years	<1 year
Maximum brood size*	6 ducklings	11 ducklings

^a Probabilities differ between Laysan and Midway; binomial test, $P < 0.001$.

On Midway, the probability of re nesting after nest failure was 0.55 (0.67 after failed first nests, $n = 9$) and the probability of re nesting after successfully raising ducklings to independence was 0.50 (0.71 after successful first nests, $n = 31$). Consistent with Reynolds et al. (2007),¹⁶ both occurrences were extremely rare on Laysan (Table 1). No females attempted three nests in a year on Laysan, whereas 24% did so on Midway (Table 1), and one female made five attempts, two of which were successful. Only one female produced two broods in a year on Laysan, whereas nearly half (44%) of the females on Midway did, and two Midway females had three successful nests in one breeding season. Although the peak of nesting occurred at the same time on both islands (March–April), the primary nesting season was longer on Midway (6–8 months) than on Laysan (4–5 months) (Fig. 3). There was an early, smaller nesting season in some years during December–January on Laysan, but not on Midway (Fig. 3).

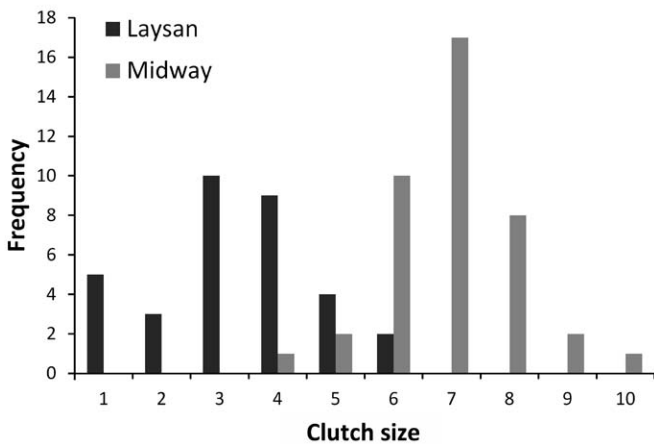


FIG. 2. Clutch sizes for first nesting attempts by radiotagged Laysan Duck hens on Laysan Island and Midway Atoll, 2004–2007.

On Midway, some females tended their broods for 2 months as on Laysan, but others deserted their broods within the first month, and a few within the first week, in order to begin another nest. In one instance, a female abandoned her 2-week-old downy brood to produce a second clutch and later united this second brood with her first. She then deserted both broods to initiate a third successful nest. The capacity of young ducklings to survive on their own in the small freshwater wetlands to which their mothers brought them soon after hatching was remarkable. An individual wetland often housed several abandoned broods at once, feeding on invertebrates and seeds in the vegetation along the edge of the wetland, on the surface of the water and, surprisingly for a dabbling duck, by diving under the water.

Thus, on Midway, Laysan Ducks exhibited reproductive traits and behaviors that have not been observed on Laysan, including different parental behavior and extreme values of traits related to reproductive effort. Besides the differences between islands, there also was considerable variation among individuals in reproductive behavior on Midway. Variation in brood attendance was noted above; clutch size varied from 4 to 10 (Fig. 2), and the number of nesting attempts from zero to 5. We suspect that we did not document the full range of trait values from our sample of radiotracked hens in 2007, which included all founders and a few F_1 birds but no F_2 birds. For example, we observed one female with 11 newly hatched ducklings. Also, we note that annual variation contributed very little to the difference between Laysan and Midway; that is, the variation among years within an island was much less than the variation between islands. For example, clutch size of first nests varied from 6.8 ± 1.0 to 7.8 ± 1.6 among 3 years on Midway and from 3.0 ± 1.1 to 3.9 ± 1.6 among 4 years on Laysan. Initial estimates of annual survival of adults (females: 0.92, males: 0.92) and fledged juveniles (0.82) are virtually identical to survival rates on Laysan.¹⁸ Thus, it is consistent differences in productivity that distinguish the two populations.

DISCUSSION

Productivity was much higher on Midway than has ever been observed on Laysan because of the production of many more offspring, with less investment in each, by females on Midway compared with those on Laysan. Intraspecific variation in reproductive effort among female anatids is often regulated by condition or energy reserves.^{25,26} Thus, a reasonable proximate explanation of the difference in productivity of the ducks on the two islands is that feeding conditions were much better on Midway than on Laysan. This could be partly attributable to lower population density on Midway, but effects of density on productivity are not a sufficient explanation of the difference between the two populations. Seavy et al. (2009) presented evidence of density-dependent population growth on Laysan,¹² but even during periods of population growth following population decline, productivity on Laysan does not approach that observed on Midway. On Midway, the population nearly doubled in size each year through 2008, yet females continued to produce multiple broods and large clutches.²³ Nor can the differences be explained by founder effects, given the genetic bottlenecks the species has experienced and the fact that life-history-trait values observed on Midway fall outside the range observed on Laysan in most cases.

If higher productivity on Midway is a consequence of better feeding conditions, what is remarkable is that Laysan Ducks have

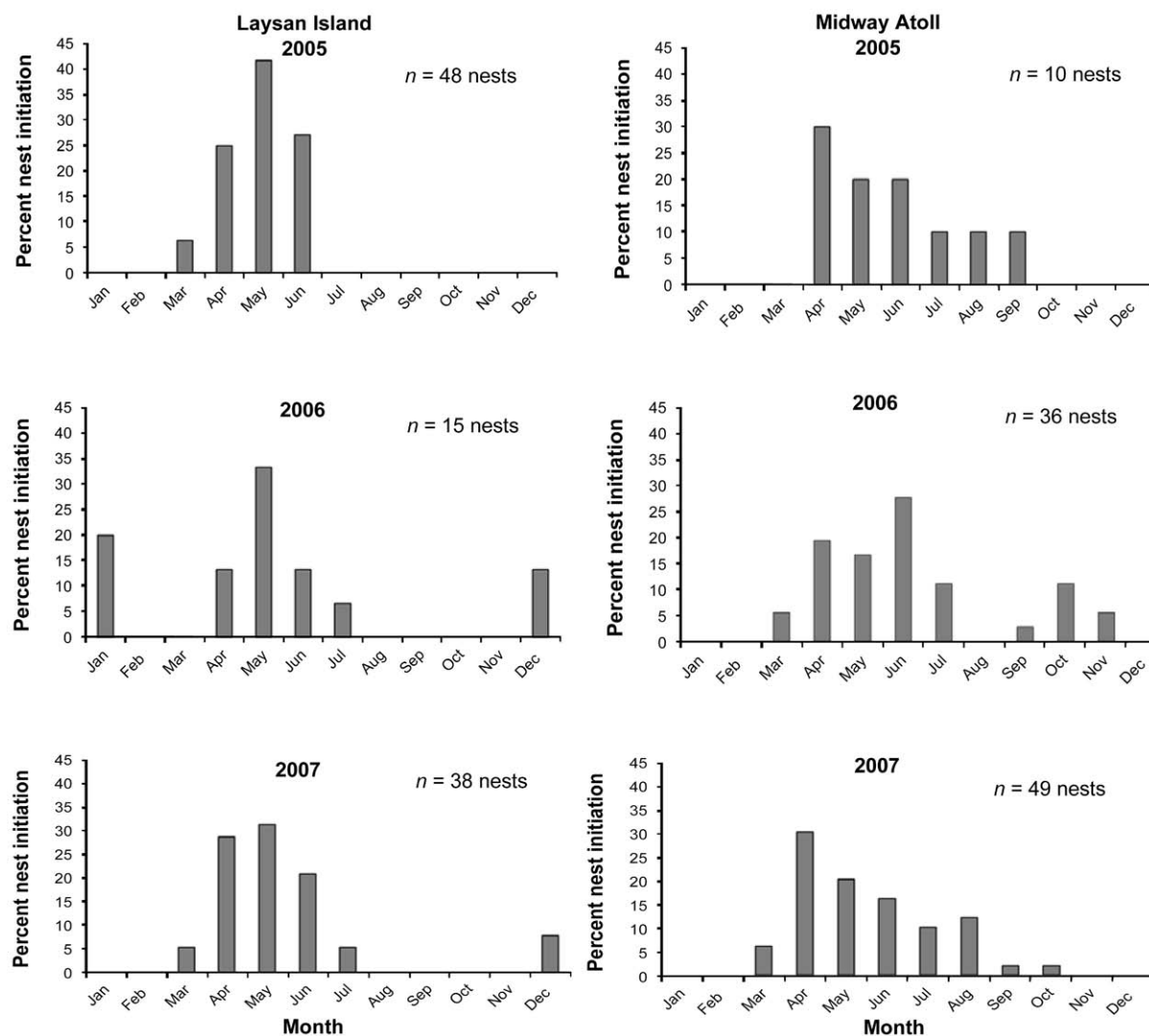


FIG. 3. Percentage of nest initiations, defined as initiation of incubation, by female Laysan Ducks by month on Laysan Island and Midway Atoll, 2005–2007.

the capacity to respond to improved feeding conditions so dramatically despite evidently having rarely, if ever, experienced the favorable foraging conditions in which these life-history-trait values presumably are adaptive on Laysan. We can only speculate about the basis of this phenotypic plasticity, but the possibilities are intriguing and potentially revealing with respect to the role of phenotypic plasticity in adaptive evolution. First, reaction norms between life history traits and environmental conditions may have evolved in this species when it formerly inhabited a diversity of environments throughout the Hawaiian Islands. The new environment represented by Midway may have revealed portions of these reaction norms unexposed on Laysan.^{1,27} Thus, the phenotypic plasticity expressed upon reintroduction to Midway may represent the ghost of selection past.¹ However, given the dominance of non-native species, it is possible that Midway represents a novel environment for Laysan Ducks. Relevant to this, a second possibility is that cryptic genetic variation may underlie the novel

phenotypes observed on Midway. Cryptic genetic variation is the standing genetic variation that does not contribute to the range of phenotypes observed in a population under standard conditions, but is available to modify a phenotype in new environments.²⁸ Pools of cryptic genetic variation may reside in hidden reaction norms, expressed only after changes in environmental conditions. Some have argued that the release of this variation in new environments is a means by which major adaptive shifts can occur and, thus, is an important force in macroevolution.^{28,29}

Ghalambor et al. (2007) noted that species introductions provide a means to test hypotheses about phenotypic plasticity,¹ and indeed such introductions often reveal plasticity in life history in particular.³⁰ The Laysan Duck may provide further such opportunities, given that other reintroductions of the species to islands quite different from either Midway or Laysan are planned in the near future. It will be particularly important to determine whether variation in the life history of Laysan Ducks can

be explained as a response to a common environmental gradient, with different ranges of environmental conditions on different islands, or represents a more complex relationship between environment and plasticity of life history traits. It may be possible to use these reintroductions as experiments to not only distinguish between mechanisms underlying phenotypic plasticity, but also to answer a critical question that we could not address, whether the novel phenotypic variation we observed provides a basis for adaptive evolution in new environments. The species is amenable to study, and it would be possible to quantify the reproductive effort and success of a large sample of females in a new population through a combination of radiotelemetry and banding. One could thus study directly the evolution of Laysan Duck life history in new environments.

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