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## PREDICTORS OF JUVENILE SURVIVAL IN BIRDS

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**ABSTRACT.**—The survival probability of birds during the juvenile period, between the end of parental care and adulthood, is highly variable and has a major effect on population dynamics and parental fitness. As such, a large number of studies have attempted to evaluate potential predictors of juvenile survival in birds, especially predictors related to parental care. Lack's hypothesis linking body reserves accumulated from parental care to the survival of naive juveniles has organized much of this research, but various other predictors have also been investigated and received some support. We reviewed the literature in this area and identified a variety of methodological problems that obscure interpretation of the body of results. Most studies adopted statistical techniques that missed the opportunities to (1) evaluate the relative importance of several predictors, (2) control the confounding effect of correlation among predictor variables, and (3) exploit the information content of collinearity by evaluating indirect (via correlation) as well as direct effects of potential predictors on juvenile survival. Ultimately, we concluded that too few reliable studies exist to allow robust evaluations of any hypothesis regarding juvenile survival in birds. We used path analysis to test potential predictors of juvenile survival of 2,631 offspring from seven annual cohorts of a seabird, the Nazca Booby (*Sula granti*). Fledging age was the most important predictor of juvenile survival: fast-growing offspring survived best, when all other variables were held constant. Offspring sex was the next most important predictor, with juvenile males (the smaller sex) surviving better than females. Hatching day, an index of body weight, and wing length also showed important predictive ability, but cohort size, culmen length, and an index of clutch size and hatching success did not. Nestling growth was compromised under poor rearing conditions: overall weight fell, the number of days needed to reach fledging status increased, and the growth of some structures, but not others, was reduced. These effects were more pronounced in females, and the higher juvenile mortality of females accounts for most of the male bias in the adult sex ratio and its attendant "mate rotation" mating system in this population. Most previous studies did not evaluate sex as a potential predictor of juvenile survival. Had we omitted sex from our models, we would have made two erroneous conclusions: that weight did not influence juvenile survival, and that small structural size enhanced it. *Received 17 May 2012, accepted 8 February 2013.*

**Key words:** body condition index, nestling growth, path analysis, reproductive success, sexual size dimorphism.

### Predictores de la Supervivencia de Aves Juveniles

**RESUMEN.**—La probabilidad de supervivencia de las aves durante el periodo juvenil, entre el final del cuidado parental y la adultez, es altamente variable y tiene un gran efecto en la dinámica poblacional y en la aptitud de los padres. Por esto, un gran número de estudios han intentado evaluar los predictores potenciales de la supervivencia de los juveniles en aves, con un foco especial en los predictores relacionados con el cuidado parental. La hipótesis de Lack en la que se relacionan las reservas corporales acumuladas por el cuidado parental con la

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supervivencia de juveniles inexpertos ha dirigido muchas de estas investigaciones, pero varios otros predictores también han sido investigados y recibido sustento. Revisamos la literatura en esta área e identificamos una variedad de problemas metodológicos que dificultan la interpretación de los datos. Muchos estudios adoptaron técnicas estadísticas que no dieron oportunidad de (1) evaluar la importancia relativa de varios predictores, (2) controlar los efectos de la correlación entre variables predictoras, y (3) explotar la información de la colinearidad al evaluar indirecta (usando correlaciones) y directamente los efectos de los predictores potenciales de la supervivencia de los juveniles. Al final concluimos que existen muy pocos estudios confiables que permitan la evaluación robusta de cualquier hipótesis sobre la supervivencia de los juveniles en aves. Usamos análisis de vías para evaluar los predictores potenciales de la supervivencia de los juveniles de 2631 descendientes de siete cohortes anuales de *Sula granti*. La edad de los volantones fue el predictor más importante de la supervivencia de los juveniles: manteniendo otras variables constantes, los polluelos que crecían rápido sobrevivieron mejor. El sexo de los polluelos fue el siguiente predictor más importante: los machos juveniles (el sexo de menor tamaño) sobrevivieron mejor que las hembras. El día de eclosión, un índice de peso corporal y la longitud del ala también mostraron una habilidad predictiva importante, pero el tamaño de la cohorte, la longitud del culmen y un índice de tamaño de nidada y éxito de eclosión no lo hicieron. El crecimiento de los polluelos se vio comprometido bajo condiciones pobres de crianza: el peso disminuyó, el número de días necesarios para alcanzar el estado de volantón aumentó y el crecimiento de algunas estructuras, aunque no de otras, se vio reducido. Estos efectos fueron más pronunciados en hembras y la mortalidad juvenil más alta en las hembras explica la mayoría del sesgo hacia los machos en la proporción de sexos de los adultos, y su consecuente sistema de apareamiento de "rotación de los machos" en esta población. La mayoría de los estudios previos no evaluaron el sexo como un predictor potencial de la supervivencia de los juveniles. Si hubiésemos omitido el sexo de nuestros modelos, habríamos alcanzado dos conclusiones erróneas: que el peso no influye en la supervivencia de los juveniles y que un tamaño corporal pequeño la mejora.

## INTRODUCTION

RESEARCH REGARDING POPULATION dynamics and life histories typically focuses on breeding success, adult survival, and adult sex ratio. These parameters are not the only important demographic effects on population growth, but they are generally easier to measure than the remaining component of the life history timeline, survival from independence to adulthood. During this interval, propagules and juveniles of both plants and animals may be inconspicuous and located away from population concentrations (e.g., in an unobservable state), making detection difficult. However, estimates of breeding success may be inaccurate if this parameter is ignored, and sex-biased juvenile survival can have profound ecological and evolutionary impacts on the population (Trivers and Willard 1973; Elgar 1990; Clutton-Brock 1991; Promislow et al. 1992; Venable 1992; Bernardo 1996; Fox and Czesak 2000; Marshall et al. 2003; Marshall and Keough 2007, 2009). For the many studies of birds, the difficulty of sexing the young of most species further complicated the issue in that group before the use of molecular sexing (Griffiths et al. 1998, Fridolfsson and Ellegren 1999). These logistical obstacles have

limited exploitation of the rich research possibilities linking parental care, offspring status at independence, and survival as a naive, prebreeding son or daughter. We begin by reviewing hypothetical predictors of juvenile survival and the logistical obstacles that complicate their study.

In an influential early contribution, Lack (1966) linked survival to a juvenile's fat reserve at the end of parental care and, thus, to the quality of its parental care. Lack focused on weight and assumed that body weight reflects the size of the fat reserve. We will refer to Lack's influential idea as the "body-reserve advantage hypothesis." He predicted a higher survival probability for heavier juveniles than for lighter ones just after leaving the nest, expecting fat reserves to buffer the food limitation that accompanies foraging inexperience. This hypothesis is invoked widely despite mixed evidence from the few studies that have made direct, invasive assessments of fat stores in relation to body weight (Thompson et al. 1993, Ardia 2005). In addition, the mean total fat content of nestling Great Tits (for scientific names of species considered in our study, see Table 1) represents only a 1-day supply of energy, assuming that the nestlings could mobilize all of their fat (Garnett 1981).

TABLE 1. Relationship between postfledging survival and several variables (body weight, size at fledging, timing of breeding, clutch size, hatching order–brood rank, growth rate, and sex) in birds. Key: “+” = positive relationship, except in the case of year, where “+” indicates that a relationship was found; “-” = negative relationship; “0” = no relationship; “~” = variable relationship with juvenile survival; and a blank cell indicates that the parameter was not examined in the study. The number of individuals (*n*) in the study is given with the number (in parentheses) of individuals or, in some cases, broods or nests that survived the period examined (if the study did not indicate the sample size of survivors, this number was estimated from survival probability), and “?” indicates that sample sizes were not reported for the study (sample sizes sometimes varied across parameters tested in a given study, and in these cases we used the smallest sample reported). “Period examined” is the duration of the study, starting at fledging, unless otherwise noted; LR = local return or recruitment as an adult. The “weight” column also indicates whether body weight was adjusted statistically for body size (BCI = body condition index; N = no, Y = yes). The symbol for sex is used to indicate the offspring sex with the higher survival probability. Under “hatching order,” late-hatched chicks have a larger chronological number than early-hatched chicks; however, with brood rank, larger and heavier chicks are often given a greater rank than small and light chicks. Therefore, studies that used brood rank in this manner had their data transposed to match the hatching-order scale. Superscript numbers after taxa refer to study citations (see footnotes). Asterisks indicate notes on the study, which are given in parentheses following the study citation. Taxonomy follows Ericson et al. (2006), Hackett et al. (2008), and Chesser et al. 2010.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
<b>GALLIFORMES</b>										
Willow Ptarmigan ( <i>Lagopus lagopus</i> ) <sup>1</sup>	1,220 (61)	LR	0* (N)		-**					
<b>ANSERIFORMES</b>										
Snow Goose ( <i>Chen caerulescens</i> ) <sup>2-6</sup>	33,644 (816)	LR			-				+	*
	2,627 (?)	LR	+ (N)*		-				+	*
	6,395 (206)	LR			-				+	*
	10,052 (740)	Postmigration**	0* (N)		-				+	0
	? (?)	?*	+ (N)		-				+	0
Emperor Goose ( <i>Chen canagica</i> ) <sup>7</sup>	574 (255)	Postmigration	+ (N)		-					0
Barnacle Goose ( <i>Branta leucopsis</i> ) <sup>8,9</sup>	263 (162)	Postmigration*	+ (N)		-					0
	489 (450)	First winter	+ (N)	+	0				+	0
Mallard ( <i>Anas platyrhynchos</i> ) <sup>10</sup>	199 (44) broods	LR			-					*
American Black Duck ( <i>Anas rubripes</i> ) <sup>11</sup>	106 (65)	Migration	+ (N)							*
Northern Shoveler ( <i>Anas clypeata</i> ) <sup>12</sup>	401 (?) broods	LR	0* (N)		-	0			+	**
Common Pochard ( <i>Aythya ferina</i> ) <sup>12</sup>	1,498 (?) broods	LR	0* (N)		-	+			+	**
Tufted Duck ( <i>Aythya fuligula</i> ) <sup>12</sup>	1,186 (?) broods	LR	0* (N)		-	+			+	**
Lesser Scaup ( <i>Aythya affinis</i> ) <sup>13</sup>	67 (18) nests	LR			-				0	*
Wood Duck ( <i>Aix sponsa</i> ) <sup>14</sup>	1,459 (67)	LR	0* (N)		0				0	**
<b>COLUMBIFORMES</b>										
Rock Pigeon ( <i>Columba livia</i> ) <sup>15,16</sup>	809 (242)	LR			-				0	
	890 (~261)	LR			0				0	

(continued)

TABLE 1. Continued.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
Eurasian Collared-Dove ( <i>Streptopelia decaocto</i> ) <sup>17</sup>	41 (26)	13 weeks	0 (Y)					0		0
<b>CUCULIFORMES</b>										
Great Spotted Cuckoo ( <i>Clamator glandarius</i> ) <sup>18</sup>	38 (24)	12 weeks	+ (N)							
<b>GRUIFORMES</b>										
Eurasian Coot ( <i>Fulica atra</i> ) <sup>19</sup>	644 (113)	1 year		+	-				+	
Houbara Bustard ( <i>Chamydotis undulata</i> ) <sup>20</sup>	92 (70)	1 year	0 (N)							0
Great Bustard ( <i>Otis tarda</i> ) <sup>21</sup>	328 (98)	1 year	+ (N)			0			+	♀
<b>PROCELLARIFORMES</b>										
Short-tailed Shearwater ( <i>Puffinus tenuirostris</i> ) <sup>22</sup>	388 (31)	LR	0 (N)	0						
Manx Shearwater ( <i>Puffinus puffinus</i> ) <sup>23</sup>	5,079 (980)	≥1 year	+ (N)		-				+	
Sooty Shearwater ( <i>Puffinus griseus</i> ) <sup>24</sup>	500 (31)	LR	+ (N)		0					
Wandering Albatross ( <i>Diomedea exulans</i> ) <sup>25</sup>	33 (14)	LR	- (Y)	+	0			0		*
	26 (17)	LR	+ (Y)	0	0			0		**
<b>SPHENISCIFORMES</b>										
Little Penguin ( <i>Eudyptula minor</i> ) <sup>26,27</sup>	45 (23)	1 year	+ (N)		-					
	606 (60)	1 year	0 (N)		0/-*	+			+	
Yellow-eyed Penguin ( <i>Megadyptes antipodes</i> ) <sup>28</sup>	2,125 (?)	≥1 year	+ (N)							
Gentoo Penguin ( <i>Pygoscelis papua</i> ) <sup>29</sup>	44 (26)	LR	0 (N)				0			
King Penguin ( <i>Aptenodytes patagonicus</i> ) <sup>30,31</sup>	65 (15)	≤4 years	0 (N)		-				+	
	2,375 (1,838)	LR	+ (Y)						+	♂
<b>CICONIIFORMES</b>										
Wood Stork ( <i>Mycteria americana</i> ) <sup>32</sup>	44 (9)	≤2 years	0* (N)						+	♀
<b>PELICANIFORMES</b>										
Little Egret ( <i>Egretta garzetta</i> ) <sup>33</sup>	3,024 (253)	LR					0		+	
<b>SULIFORMES</b>										
European Shag ( <i>Phalacrocorax aristotelis</i> ) <sup>34</sup>	13,086 (1,377)	≥3 years			-	+			+	

(continued)

TABLE 1. Continued.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
Cape Gannet ( <i>Morus capensis</i> ) <sup>35</sup>	1,004 (991)	?*	+**(N)		-					
Nazca Booby ( <i>Sula granti</i> ) <sup>36</sup>	2,080 (995)	LR	+(N)	+	-			+	0	♂
<b>CHARADRIIFORMES</b>										
Herring Gull ( <i>Larus argentatus</i> ) <sup>37,38</sup>	10,090 (1,479)	LR			0					
	27,115 (708)	LR			-	-				
Western Gull ( <i>Larus occidentalis</i> ) <sup>39</sup>	1,056* (193)	LR			-	+	-		+	
Black-legged Kittiwake	904 (94)	LR				+	-	+		
( <i>Rissa tridactyla</i> ) <sup>40,41</sup>	4,059 (477)	1 year					-	+		
Common Tern ( <i>Sterna hirundo</i> ) <sup>42,43</sup>	236 (106)	2 years	+(N)		0				+	0
	236 (199)	Departure	0 (N)					+		0
Sooty Tern ( <i>Onychoprion fuscatus</i> ) <sup>44</sup>	1,127 (20)	≥22 years*	0 (N)		-					
Sandwich Tern	3,365 (413)	LR	0 (N)						+	
( <i>Thalasseus sandvicensis</i> ) <sup>45</sup>										
Black-fronted Tern	44 (36)	4 weeks	+(N)	+				0	*	
( <i>Chlidonias albostratus</i> ) <sup>46</sup>										
Common Guillemot	13,841 (278)	≥1 year	0 (N)		0					
( <i>Uria aalge</i> ) <sup>47-49</sup>	1,277 (313)	≥6 months*	0 (Y)		-			0	+	
	9,025 (5,054)	1 year	0 (Y)*		-			+	+	
Thick-billed Murre ( <i>Uria lomvia</i> ) <sup>50</sup>	138 (29)	4-5 years	0* (N)		0**					
Razorbill ( <i>Alca torda</i> ) <sup>51</sup>	1,461 (72)	LR	0* (N)		0					
Ancient Murrelet	4,045 (53)	LR	+* (N)		+					
( <i>Synthliboramphus antiquus</i> ) <sup>52</sup>										
Atlantic Puffin ( <i>Fratercula arctica</i> ) <sup>53</sup>	268 (58)	≥6 months	0 (N)		0			0		
Tufted Puffin ( <i>Fratercula cirrhata</i> ) <sup>54</sup>	133 (35)	LR	+(N)	+	-				+	
Great Skua ( <i>Stercorarius skua</i> ) <sup>55</sup>	420 (291)	≤1 year			-					
Parasitic Jaeger	1,313 (38)	LR	+(N)		-					
( <i>Stercorarius parasiticus</i> ) <sup>56</sup>										
Eurasian Oystercatcher	120 (46)	LR	0 (N)	0	0			0		
( <i>Haematopus ostralegus</i> ) <sup>57</sup>										
<b>CORACIIFORMES</b>										
Laughing Kookaburra	162 (9)	LR	+(N)	0						0
( <i>Dacelo novaeguineae</i> ) <sup>58</sup>										
Middle Spotted Woodpecker	39 (12)	46 days	+(Y)		0					0
( <i>Dendrocopos medius</i> ) <sup>59</sup>										

(continued)

TABLE 1. Continued.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
<b>STRIGIFORMES</b>										
Burrowing Owl	32 (18)	3 months	+ (N)		0	0			+	0
<i>(Athene cunicularia)</i> <sup>60,61</sup>	40 (22)	Migration	0 (Y)			0			0	
Tawny Owl ( <i>Strix aluco</i> ) <sup>62</sup>	502* (104)	LR				–				
<b>ACCIPITRIFORMES</b>										
Eurasian Sparrowhawk	240 (58)	28 days	0 (N)			0		0		*
<i>(Accipiter nisus)</i> <sup>63</sup>										
Northern Goshawk	89 (64)	12 weeks	+ (N)		0	0			0	♂*
<i>(Accipiter gentilis)</i> <sup>64</sup>										
Egyptian Vulture	658 (?)	≥1 year	0 (Y)						0	0
<i>(Neophron percnopterus)</i> <sup>65</sup>										
<b>FALCONIFORMES</b>										
Prairie Falcon ( <i>Falco mexicanus</i> ) <sup>66</sup>	152 (105)	35 days	0 (Y)		0	0			0	0
<b>PASSERIFORMES</b>										
Eastern Kingbird	102 (25)	LR	0 (N)	0	–	–			0	*
<i>(Tyrannus tyrannus)</i> <sup>67</sup>	94 (21)	LR	0 (N)	0	0	–			+	**
Black-crowned Antshrike	24 (11)	LR	+ (N)			–				0
<i>(Thamnophilus atrinucha)</i> <sup>68</sup>										
Brown Thornbill ( <i>Acanthiza pusilla</i> ) <sup>69</sup>	159 (37)	LR	+ (Y)		0	0	0		0	♂*
Spotted Antbird	81 (37)	50 days	0 (N)			–				
<i>(Hylophylax naevioides)</i> <sup>70</sup>										
Great Tit ( <i>Parus major</i> ) <sup>71–84</sup>	? (?)*	3 months	+ (N)		–	+			+	
	466 (125)	11 weeks		+	0	0				*
	541 (69)	≥3 months	+ (N)	+						
	1,482 (270) <sup>74</sup>	Winter	+ (N)	+						
	1,482 (270) <sup>74</sup>	LR			–	–				
	3,575 (?) <sup>75</sup>	LR—Hoge Veluwe	+ (N)		0				+	♂*
	3,675 (?) <sup>75</sup>	LR—Vlieland	+ (N)		0				+	♂*
	5,907 (341)	LR	+ (Y)		–	–				
	137 (14)	LR	+ (N)		–					

(continued)

TABLE 1. Continued.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
Great Tit ( <i>Parus major</i> ) <sup>71-84</sup>	3,932 (285)	LR	+ (N)		-				+	♀*
	? (?)*	LR	+ (N)							
	2,051 (184)	LR	+ (N)		~*				0	
	3,147 (288)	≥1 year	+ (N)		0				+	
	273 (19)	LR	0 (Y)		0	0			0	
	3,106 (734)	3 months	+ (N)						+	
Coal Tit ( <i>Periparus ater</i> ) <sup>84,85</sup>	266 (141)	20 days	+ (N)		-	0				
	76 (40)	20 days	+ (N)		-	0				
	1,086 (114)	LR			-					0
Blue Tit ( <i>Cyanistes caeruleus</i> ) <sup>86-88</sup>	878	≥3 months	+ (N)				0			
	(68)									
	? (?)*	≥3 months			-	+			+	
	1,204 (119)	First winter or more	+ (N)	+						♂
Long-tailed Tit ( <i>Aegithalos caudatus</i> ) <sup>89</sup>	652 (?)	Overwinter	+ (N)		0	0			+	♂*
Common House Martin ( <i>Delichon urbica</i> ) <sup>90</sup>	505 (35)	1 year	0 (Y)		0*	+				
Purple Martin ( <i>Progne subis</i> ) <sup>91</sup>	3,990 (1,077)	1 year			-	-			+	
Barn Swallow ( <i>Hirundo rustica</i> ) <sup>92,93</sup>	218 (?)	38 days	0 (N)	+	-				+	
	243 (?)	38 days			-				+	
Tree Swallow ( <i>Tachycineta bicolor</i> ) <sup>94,95</sup>	37 (14) broods*	LR	0 (N)	0				0		
		LR	+ (N)	0		-	0			
Cliff Swallow ( <i>Petrochelidon pyrrhonota</i> ) <sup>96</sup>	5,122* (?)	1 year			-**				+	
Sociable Weaver ( <i>Philetairus socius</i> ) <sup>97</sup>	435 (?)	4 months	+/- (N)*	0						
Stitchbird ( <i>Notiomystis cincta</i> ) <sup>98</sup>	594 (?)	LR	0 (N)		0					
Akepa ( <i>Loxops coccineus</i> ) <sup>99</sup>	71 (27)	≥1 year	+ (N)	0						
American Dipper ( <i>Cinclus mexicanus</i> ) <sup>100</sup>	82 (10)	LR	0 (Y)	0	0	0		0	0	0
Collared Flycatcher ( <i>Ficedula albicollis</i> ) <sup>101,76,102</sup>	2,135 (1,826)	LR	+ (N)	+		-				
	7,560 (853)	LR	+ (Y)			0				
	2,065 (1,764)	LR	+ (Y)	+		-	0		+	

(continued)



TABLE 1. Continued.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
European Pied Flycatcher ( <i>Ficedula hypoleuca</i> ) <sup>103-107</sup>	918 (145)	LR	0 (Y)	0		-				0*
	419 (53)	LR	+ (N)	0		-				0
	303 (18)	LR	0 (N)			0			+	
	491 (36)	LR	0 (N)			0			0	
	1,705 (?)	LR		+						
Puff-throated Bulbul ( <i>Alophoixus pallidus</i> ) <sup>108</sup>	54 (33)	8 weeks	0 (N)		0				0	0
Ovenbird ( <i>Seiurus aurocapilla</i> ) <sup>109</sup>	51 (33)	51 days	+ (Y)		-	0			0	
Worm-eating Warbler ( <i>Helmitheros vermivorum</i> ) <sup>109</sup>	60 (40)	31 days	+ (Y)		+	-			0	
Karoo Scrub Robin ( <i>Cercotrichas coryphaeus</i> ) <sup>110</sup>	167 (129)	3 weeks	+ (N)		0	0				
House Sparrow ( <i>Passer domesticus</i> ) <sup>111-113</sup>	3,400 (100)	LR	+ (N)		0	0				
	408 (108)	LR	+ (Y)	+	+	0				
	793 (152)	LR	+ (N)		0	0			0	♀
Savannah Sparrow ( <i>Passerculus sandwichensis</i> ) <sup>114,115</sup>	596 (25)	LR	0 (N)	0	0	0		0		
	221 (37)	LR	+ (N)		-				0	0
Song Sparrow ( <i>Melospiza melodia</i> ) <sup>116</sup>	1,193 (774)	5 months	+ (Y)		0		0		+	
Lark Bunting ( <i>Calamospiza melanocorys</i> ) <sup>117</sup>	167 (27)	22 days	0 (Y)		+/-*		-**		+	***
Dunnock ( <i>Prunella modularis</i> ) <sup>118</sup>	319 (229)	2-3 weeks	+ (N)						0	
Yellow-eyed Junco ( <i>Junco phaeotus</i> ) <sup>119</sup>	206 (45)	36 days	0 (N)						0	
Cactus Wren ( <i>Campylorhynchus brunneicapillus</i> ) <sup>120</sup>	81 (?)	4-6 weeks	+ (N)						+	
Dickcissel ( <i>Spiza americana</i> ) <sup>121,122</sup>	155 (86)	58 days	+ (N)		0	0			0	
	53 (20)	30 days	0 (N)						0	
Wood Thrush ( <i>Hylocichla mustelina</i> ) <sup>123,124</sup>	49 (21)	8 weeks	0 (N)		0					
	941 (48)*	LR	0 (Y)	0	-	0		0		
Eurasian Blackbird ( <i>Turdus merula</i> ) <sup>125,126</sup>	417 (41)	LR	+ (N)*							
	190 (107)	20 days	+ (N)*			0				
Red-backed Shrike ( <i>Lanius collurio</i> ) <sup>127</sup>	176 (32)	LR	0 (Y)	0	-	+			+	

(continued)

TABLE 1. Continued.

Taxon	<i>n</i>	Period examined	Weight (BCI)	Size	Timing of breeding	Clutch/ brood size	Hatching order/ brood rank	Growth rate	Cohort/ year	Sex
Eastern Meadowlark ( <i>Sturnella magna</i> ) <sup>128,121</sup>	50 (29)	90 days	+ (N)						0	
	107 (77)	72 days	+ (N)		0	0			0	
European Starling ( <i>Sturnus vulgaris</i> ) <sup>129,130</sup>	121 (50)	42 days	0 (N)							
	157 (?)	11 weeks	+ (N)		0					
Spotless Starling ( <i>Sturnus unicolor</i> ) <sup>131</sup>	291 (32)	LR		?*	?	?			+	?
Hooded Crow ( <i>Corvus cornix</i> ) <sup>132</sup>	162 (62)	Dispersal	+ (N)		-	+				
Carrion Crow ( <i>Corvus corone</i> ) <sup>133</sup>	82 (34)	Overwinter	0 (N)*	+						0
Florida Scrub-Jay ( <i>Aphelocoma coerulescens</i> ) <sup>134</sup>	63 (38)	40 days	+ (N)	+			-			
European Magpie ( <i>Pica pica</i> ) <sup>135-137</sup>	50 (10)	≥9 months	0 (N)		0					
	39 (29)	50 days	+ (N)	+		0		0		0
	309 (36)	LR	+ (N)		-					0

<sup>1</sup>Martin and Hannon 1987 (\*weight at 1–7 days, categorized as light, medium, or heavy; \*\*comparison of first and replacement clutches); <sup>2</sup>Cooke et al. 1984 (\*only females in the analysis); <sup>3</sup>Cooch 2002 (\*only females in the analysis); <sup>4</sup>Reed et al. 2003 (\*only females in the analysis); <sup>5</sup>Menu et al. 2005 (\*mean mass and fledging date of a cohort were used to predict cohort survival probability); <sup>6</sup>Francis et al. 1992 (\*survival based on band recoveries from hunters); <sup>7</sup>Schmutz 1993; <sup>8</sup>Owen and Black 1989; <sup>9</sup>Shorrocks et al. 1998; <sup>10</sup>Dzus and Clark 1998 (\*only females in the analysis); <sup>11</sup>Longcore et al. 1991 (\*only females in the analysis); <sup>12</sup>Blums et al. 2002 (\*mean weight of brood on hatching day; \*\*examined females only); <sup>13</sup>Dawson and Clark 2000 (\*only females in the analysis); <sup>14</sup>Hepp et al. 1989 (\*weight on hatching day; \*\*examined females only); <sup>15</sup>Hetmański 2007; <sup>16</sup>Hetmański and Barkowska 2008; <sup>17</sup>Eraud et al. 2011; <sup>18</sup>Soler et al. 1994; <sup>19</sup>Brinkhof et al. 1997; <sup>20</sup>Chargé et al. 2011; <sup>21</sup>Martin et al. 2007; <sup>22</sup>Meathrel and Carey 2007; <sup>23</sup>Perrins 1966, Perrins et al. 1973; <sup>24</sup>Sagar and Horning 1998; <sup>25</sup>Weimerskirch et al. 2000 (\*males only in the analysis, \*\*females only in the analysis); <sup>26</sup>Reilly and Cullen 1982; <sup>27</sup>Johannessen et al. 2003 (\*interaction between laying date and clutch size—singletons had negative relationship); <sup>28</sup>McClung et al. 2004; <sup>29</sup>Williams and Croxall 1991; <sup>30</sup>Olsson 1997; <sup>31</sup>Saraux et al. 2011; <sup>32</sup>Hylton et al. 2006 (\*measured ~1 month before fledging); <sup>33</sup>Hafner et al. 1998; <sup>34</sup>Harris et al. 1994; <sup>35</sup>Jarvis 1974 (\*time frame is uncertain because comparison was between fledgling mean weight (including dead birds) and mean weight of dead band recoveries, \*\*underweight young died shortly after leaving the colony); <sup>36</sup>present study; <sup>37</sup>Nisbet and Drury 1972; <sup>38</sup>Parsons et al. 1976; <sup>39</sup>Spear and Nur 1994 (\*total number hatching); <sup>40</sup>Coulson and Porter 1985; <sup>41</sup>Cam et al. 2003; <sup>42</sup>Braasch et al. 2009; <sup>43</sup>Schauroth and Becker 2008; <sup>44</sup>Fearé 2002 (\*long-term survival); <sup>45</sup>Stienen and Brenninkmeijer 2002; <sup>46</sup>Keedwell 2003 (\*years pooled due to small sample sizes); <sup>47</sup>Hedgren 1981; <sup>48</sup>Harris et al. 1992 (\*all analyses were repeated in birds known to be alive at 2 years, and results did not change); <sup>49</sup>Harris et al. 2007; <sup>50</sup>Hipfner 2001 (\*weight at ~15 days old, \*\*comparison between first and replacement broods); <sup>51</sup>Lloyd 1979 (\*weight was not tested directly but was inferred from hatching date’s relationship with survival); <sup>52</sup>Gaston 1997 (\*weight at 1–4 days old); <sup>53</sup>Harris and Rothery 1985; <sup>54</sup>Morrison et al. 2009; <sup>55</sup>Catry et al. 1998; <sup>56</sup>Phillips and Furness 1998; <sup>57</sup>Kersten and Brenninkmeijer 1995; <sup>58</sup>Legge 2002; <sup>59</sup>Robles et al. 2007; <sup>60</sup>Todd et al. 2003; <sup>61</sup>Davies and Restani 2006; <sup>62</sup>Sasvári and Hegyi 2010 (\*number of clutches that produced at least one fledgling; returning number is individuals); <sup>63</sup>Newton and Moss 1986 (\*males in all-male broods and female in all-female broods survived better than others of their sex in two-sex broods); <sup>64</sup>Wiens et al. 2006 (\*females with low mass were less likely to survive than males with low mass); <sup>65</sup>Grande et al. 2009; <sup>66</sup>McFadzen and Marzluff 1996; <sup>67</sup>Dolan et al. 2009 (\*only males in the analysis, \*\*only females in the analysis); <sup>68</sup>Tarwater et al. 2011; <sup>69</sup>Green and Cockburn 2001 (\*attributed to female-biased dispersal); <sup>70</sup>Styrsky et al. 2005; <sup>71</sup>Perrins 1965 (\*sample sizes were not given, but were ≥10,000), <sup>72</sup>Dhondt 1979 (\*examined male survival only, owing to female-biased dispersal); <sup>73</sup>Garnett 1981; <sup>74</sup>Smith et al. 1989; <sup>75</sup>Tinbergen and Boerlijst 1990 (\*attributed to female-biased dispersal); <sup>76</sup>Lindén et al. 1992; <sup>77</sup>Verhulst and Tinbergen 1991, Verhulst et al. 1995; <sup>78</sup>Verboven and Visser 1998 (\*attributed to female-biased recapture probability at nest boxes); <sup>79</sup>Both et al. 1999 (\*sample sizes not given, but were ≥2,800); <sup>80</sup>Monrós et al. 2002 (\*early, intermediate, or late hatching individuals were favored in different years); <sup>81</sup>Greño et al. 2008; <sup>82</sup>Norte et al. 2008; <sup>83</sup>van Noordwijk et al. 1988; <sup>84</sup>Naef-Daenzer et al. 2001; <sup>85</sup>Dietrich et al. 2003; <sup>86</sup>Nur 1984; <sup>87</sup>Svensson 1997 (\*2,272 banded fledglings, but sample sizes varied between analyses); <sup>88</sup>Räberg et al. 2005; <sup>89</sup>MacColl and Hatchwell 2003 (\*attributed to female-biased dispersal); <sup>90</sup>Christe et al. 2001 (\*comparison between first and second broods); <sup>91</sup>Tarof et al. 2011; <sup>92</sup>Grüebler and Naef-Daenzer 2010; <sup>93</sup>Grüebler and Naef-Daenzer 2008; <sup>94</sup>De Steven 1980 (\*all analyses used mean brood values); <sup>95</sup>Shutler et al. 2006; <sup>96</sup>Brown and Brown 1999 (\*nonfumigated nests; \*\*result was variable, but overall earlier hatching date had higher survival than late

(continued)

TABLE 1. Continued.

hatch); <sup>97</sup>Covas et al. 2002 (\*stabilizing selection on weight); <sup>98</sup>Low and Pärt 2009; <sup>99</sup>Medeiros and Freed 2009; <sup>100</sup>Middleton and Green 2008; <sup>101</sup>Gustafsson and Sutherland 1988; <sup>102</sup>Kruuk et al. 2002; <sup>103</sup>Potti and Montalvo 1991 (\*sex ratio was assumed to be even at fledging but was unknown); <sup>104</sup>Potti et al. 2002; <sup>105</sup>Lobato et al. 2005; <sup>106</sup>Moreno et al. 2005; <sup>107</sup>Alatalo and Lundberg 1986; <sup>108</sup>Sankamethawee et al. 2009; <sup>109</sup>Vitz and Rodewald 2011; <sup>110</sup>Lloyd et al. 2009; <sup>111</sup>Ringsby et al. 1998; <sup>112</sup>Schwagmeyer and Mock 2008; <sup>113</sup>Cleasby et al. 2010; <sup>114</sup>Ross and McLaren 1981; <sup>115</sup>Wheelwright et al. 2003; <sup>116</sup>Hochachka and Smith 1991; <sup>117</sup>Yackel Adams et al. 2006 (\*quadratic effect, \*\*rank within brood was only important during drought year, \*\*\*year effect = drought severity); <sup>118</sup>Davies 1986; <sup>119</sup>Sullivan 1989; <sup>120</sup>Simons and Martin 1990; <sup>121</sup>Suedkamp Wells et al. 2007; <sup>122</sup>Berkeley et al. 2007; <sup>123</sup>Anders et al. 1997; <sup>124</sup>Brown and Roth 2004 (\*not all banded nestlings were measured, so this number may include survivors with no measure); <sup>125</sup>Magrath 1991 (\*other variables, such as the effect of brood size, year, etc. on survival were only examined in the 2 weeks after fledging, not until return, so only weight is shown here); <sup>126</sup>Snow 1958 (\*reexamination of data revealed significant positive correlation between probability of survival and mass); <sup>127</sup>Müller et al. 2005; <sup>128</sup>Kershner et al. 2004; <sup>129</sup>Stromborg et al. 1988; <sup>130</sup>Kremnitz et al. 1989; <sup>131</sup>López-Rull et al. 2011 (\*all variables designated with a “?” were analyzed in this study, but implementation of statistical method was incorrect and not interpretable); <sup>132</sup>Loman 1977; <sup>133</sup>Richner 1992 (\*the effect of mass on overwinter survival was not tested directly; fledglings of food-supplemented parents were heavier, but probability of survival was not different between supplemented and control pairs); <sup>134</sup>Mumme 1992; <sup>135</sup>Ponz Miranda et al. 2007; <sup>136</sup>Husby and Slagsvold 1992; <sup>137</sup>Molina-Morales et al. 2012.

Instead, Garnett (1981) suggested that selection on juveniles targeted overall size (a correlate of weight) and that larger body size confers an advantage in physical competition for resources, the “size advantage hypothesis.” Lack’s and Garnett’s hypotheses both predict positive correlations between weight, size, and juvenile survival, and data from most studies of passerines have been interpreted to show the high weight–high survival pattern (Table 1), with measurements generally taken at fledging (= nest-leaving, which is not necessarily the end of parental care), for logistical reasons. In this monograph, we review the literature with respect to reported relationships between fledging size–weight and survival, taking into account other predictors of survival, methodological considerations, and data quality. For now, we note that many studies do not separate the effects of weight and structural size on juvenile survival (although this can be attempted with path analysis; see below), preventing a contrast of the two hypotheses. Most examine the effects of weight and ignore structural size, or attempt to control the effect of body size on survival statistically to test the body-reserve advantage hypothesis (Table 1).

Body measurements around the time of nest-leaving provide the only predictors of juvenile survival in many studies of birds, and onerous hidden assumptions in such an analysis can easily be overlooked. For example, young of many ducks and other precocial species leave the nest well before independence from their parents, at a small fraction of their eventual weight and size; the assumption that no meaningful variation in development occurs after that time is tenuous. Consider also seabirds, which have provided mixed results and often fail to show a positive correlation between weight at fledging and subsequent survival (Table 1). The timing of any effect of weight on juvenile survival is the focus of some studies, but our interest is broader: Does weight at the end of parental care affect survival to adulthood, the most poorly understood part of the demographic timeline? Several factors might obscure such an effect if it did exist. The life history syndrome of many seabirds includes long adult life span, small brood size, and a lengthy nestling period (Weimerskirch 2002). In their variable and unpredictable marine environment, potentially long-lived seabirds are expected to evolve mechanisms to minimize personal costs of reproduction and to shunt such costs to their offspring (Mauck and Grubb 1995). Selection on nestlings then favors plastic growth

and other responses to food shortage, so two birds at the end of parental care may have reached similar body weights via dramatically different nutritional and developmental histories. Body weight at that point may be convenient to measure as a one-time effort but may be a poor predictor of an individual's physiological, behavioral, and cognitive capabilities that will influence its performance in the near future if different newly independent individuals have survived quite different degrees of stress during the period of dependence (Blount et al. 2003, Pravosudov et al. 2005, Pravosudov and Kitaysky 2006, Arnold et al. 2007a). For species that provide parental care after nest-leaving, a young bird's status at nest-leaving may have little relevance for its survival after independence, as Stienen and Brenninkmeijer (2002) proposed for seabirds (and probably applies to other taxa with parental care after nest-leaving, particularly precocials). Finally, the contrast of seabirds and non-seabirds is, in part, one of single-chick broods with multi-chick broods, with attendant differences related to sibling competition that influence development, especially in cases when offspring are confined together in a "nursery" (Mock and Parker 1997). Whatever the reasons, body weight at fledging provides a poor indicator of postfledging performance in seabirds with postfledging care, and the gap in our understanding of this aspect of bird life history partly motivated our study.

Body size and weight predict juvenile survival in many bird species, so sex-biased survival might be expected in species with sexual size dimorphism (= dimorphism in weight and/or nonweight size). Several species of mammals and birds have sex-biased survival of male and female offspring, especially during the period of parental care (Clutton-Brock 1991). In some cases, these species show no sexual size dimorphism (identifying sex *per se*, and not sexual size dimorphism specifically as a cause of survival), but sex-biased survival before adulthood is observed more frequently in sexually size-dimorphic species (Clutton-Brock 1991). The larger sex sometimes shows lower survival, due to starvation during or after the period of parental care, probably linked to its higher food requirements (Howe 1977, Cronmiller and Thompson 1981, Fiala and Congdon 1983, Røskaft and Slagsvold 1985, Slagsvold et al. 1986, Teather and Weatherhead 1989, Torres and Drummond 1997, Martín et al. 2007). In other species, the larger sex can convert its larger dimensions into a competitive advantage against nestmates and have higher

survival when competing with siblings (Breitwisch 1989, Olsen and Cockburn 1991, Mulvihill et al. 1992, Anderson et al. 1993, Arroyo 2002, Hipkiss et al. 2002). These effects of sex-specific physical dimension can reasonably be expected to extend into the juvenile period, but sex has not been available as a predictor in most studies to date.

Factors other than weight, size, and sex can influence juvenile survival, including hatching date, hatching order, brood size, and nestling growth rate (Table 1). These factors are related to parental care and are correlated with each other. Lack (1954) proposed that birds rear young at the best time of year and that the positively skewed distribution of laying dates indicates that selection favors early breeding. Early breeding may allow offspring to fledge during periods of resource abundance, which may buffer them as they learn to forage for themselves. Young fledged earlier in the breeding season may also have more time to improve their foraging skills and acquire fat reserves prior to winter or migration than young fledged late in the breeding season. Many studies give general support to the early breeding hypothesis (Table 1).

Hatching order has been found to influence, to varying degrees, nestling survival in passerines (e.g., Gibbons 1987, Magrath 1989, Forbes et al. 2002), seabirds (e.g., Drummond et al. 1986), raptors (Newton 1979), egrets (e.g., Fujioka 1985), grebes (Kloskowski 2003), and others (Mock and Parker 1997) because late-hatched chicks may not be able to obtain adequate nutrients as a result of competition (aggressive, in some cases) with larger, and perhaps more coordinated, older siblings. Constant bullying of younger siblings by older siblings can establish a dominance hierarchy within broods through trained winning and losing (Valderrábano-Ibarra et al. 2007), and stress from bullying can generate effects that carry over into adulthood (Müller et al. 2008, 2011; Grace et al. 2011). These effects of hatching order and subsequent sibling competition seem likely to influence survival from fledging to adulthood, although few studies have addressed this hypothesis and most of those that did found no relationship (Table 1).

Brood size is also thought to influence juvenile survival, although causal relationships may be complex. High-quality parents may be able to produce and raise more offspring than low-quality parents (e.g., Lescroël et al. 2010); in this case, large brood size is associated with high survival. However, offspring from large broods have more competition for parental care than offspring from

smaller broods. Accordingly, studies that have investigated brood size and juvenile survival have had mixed results. Some studies have found a positive and others a negative relationship between brood size and juvenile survival, even in different populations of the same species (Table 1).

Growth rate is expected to influence juvenile survival if fast growth indicates low stress during the developmental period. Offspring that do not receive adequate nutrition during development may be expected to have slower growth than consistently well-fed offspring of the same population (Gebhardt-Henrich and Richner 1998). To date, few studies of birds have investigated the hypothesis that growth rate from hatching to independence influences subsequent survival (Table 1).

Adults must accumulate enough resources to attain and maintain breeding condition (Perrins 1970), and high-performing parents may be expected to breed early; to have large brood sizes, characteristic brood sex ratios, and short nestling periods (i.e., fast growth); and to produce large and/or heavy offspring, compared to low-performing parents. The correlation of these variables often impedes investigations regarding the relative importance of individual predictive factors on juvenile survival. As a consequence, many studies have examined only one or a few of these possible influences on juvenile survival (Table 1). Even fewer studies have included sex-specific survival analysis, reflecting logistical (e.g., variable dispersal, long period between independence and recruitment) and technical challenges (e.g., sex determination, inability to collect large sample sizes, correlated independent variables). Variable natal dispersal distance (movement from the natal site to a different one for first breeding) complicates the estimation of juvenile survival in many species, and sex-biased dispersal (Greenwood 1980) can bias survival estimates. Juvenile survival will be underestimated unless natal philopatry is high or dispersal areas are identified and monitored.

*Dealing with collinearity among predictors.*—Many, and perhaps most, predictors of interest for juvenile survival will be correlated; avoiding misleading results due to collinearity among predictors is a main focus of this monograph. If correlated predictors are used in a typical generalized-linear-modeling approach (e.g., capture–mark–recapture [CMR]), the standard errors of the regression coefficients can be inflated, leading to correlated errors in the regression coefficients themselves, obscuring the relative importance of the predictors (Licht 1995, Graham

2003, Gimenez et al. 2009). Many studies avoid this problem by using a stepwise method, but the stepwise technique often does not select the best set of predictors and can generate idiosyncratic results (Licht 1995, Lukacs et al. 2010). Other studies have avoided collinearity problems by examining only a few predictors (Table 1), using separate regression analyses, which can reduce the power of the analysis, or combining related predictors using principal component analysis, even though the resulting principal components might not be those most related with the outcome variable (weight, in this case; Gimenez et al. 2009). None of these techniques can assess the relative importance of several correlated predictor variables.

Path analysis, a type of structural equations modeling that does not include latent variables, allows simultaneous examination of correlated predictor variables. Path analysis not only minimizes the confounding effect of collinearity, but actually exploits correlations between predictors to infer both direct and indirect relationships. It can accommodate both ordinal and dichotomous variables (Byrne 2009, Garson 2012). Below, we enumerate other advantages of path analysis and use an extensive data set to compare the performance of path analysis against that of some other statistical approaches and show empirically that path analysis was the best choice.

*What do we know about juvenile survival in birds from the best studies?*—Reviewing the studies of predictors of postfledging survival completed thus far (Table 1) presents some problems in interpretation, for several reasons. The period over which survival was monitored varied widely, including fledging (defined as nest-leaving in most studies) to independence, to dispersal, to migration, and to first winter (Table 1). Studies over these intervals provide important information on postfledging survival but cover only part of the life span between independence from parents and the start of breeding. Many studies that follow individual fledglings to adulthood covered only local survival (e.g., Hochachka and Smith 1991, MacColl and Hatchwell 2003), so dispersal cannot be distinguished from cases of mortality. While this is valuable information for studies of local population dynamics, it should not be equated with juvenile survival. Some studies have justified using local survival as a proxy for survival to breeding age when natal dispersal within the study area was not related to the parameters measured (e.g., Lindén et al. 1992); however, predictors of juvenile survival could covary with dispersal distance, so excluding results from

long-distance dispersers could bias survival estimates. Some studies used several univariate tests (e.g., Weimerskirch et al. 2000) to estimate a parameter's influence on survival, which (1) reduces the power of the test compared with a multivariate test, (2) does not determine the relative importance of each variable on juvenile survival, and (3) risks Type 1 error unless corrected for multiple comparisons. Juvenile survival, particularly for long-lived species with delayed maturation, is rarely estimated robustly, considering unobservable states and detection rates. Limitations such as these may obscure important signal that might be more apparent when considering only the highest-quality studies in the group.

Very few studies controlled offspring sex in their analyses (Table 1), in most cases because of understandable difficulties in detecting offspring sex before convenient molecular methods became available. Sex differences introduce fundamental heterogeneities into biological data sets, and when the sexes are pooled the investigator faces the potential for noise or biased results. For example, if the heavier of the sexes has higher juvenile survival resulting from its habitat preference, behavior, or another factor, but fledging weight itself is unrelated to survival, then weight may appear erroneously to be an informative predictor of survival. Sexual weight dimorphism is common in birds (Székely et al. 2007), including the subjects of some of the most influential studies in Table 1, such as Great Tits (males 6% heavier at fledging than females; Both et al. 1999). Of course, weight is only one potential axis of variation distinguishing the sexes.

To address these issues of quality control, we identified studies in Table 1 that met a set of stringent criteria, to determine whether this subset suggests a different general conclusion than consideration of all studies, regardless of quality. The criteria are as follows. (1) Offspring characters of individual offspring (not pooled by brood or other group) were used as predictor variables. (2) Morphological measures of individual offspring were measured near the end of parental care or when growth was approximately complete (often around the time of nest-leaving in altricial species). (3) Individual fledglings were followed from independence or just before independence to breeding age (survival to some point in the juvenile period does not meet this criterion). (4) There was high natal philopatry or, alternatively, dispersal areas were included in the analysis. (5) Offspring sex was known and included in the analysis. (6) Sample size was sufficient for the

analysis attempted (for example, logistic regression requires that the smaller of the classes of the dependent variable have  $\geq 10$  cases per parameter in the model; Peduzzi et al. 1996). (7) No highly correlated predictors were used in the same model (Graham 2003) unless the model was designed to accommodate them. (8) If multiple statistical tests were performed, the critical values were adjusted for multiple comparisons. (9) Known surviving birds were not considered nonsurvivors (this problem arises, for example, when "surviving" birds are limited to dead band recoveries after the juvenile period, culls, or a subset of the living banded population). (10) More than 1 year of data was used in the analysis, because differences in the quality of the year might alter the relative importance of some variables on survival. And (11) the study was done under approximately natural conditions (e.g., supplemental food was not supplied).

We reduced Table 1 to only those studies that meet these criteria (for explanation of decisions to include or exclude particular studies, see Table S1 in the online supplemental material; see Acknowledgments), summarizing them by order (Table 2), longevity (annual adult survival probability; Table 3), and developmental mode (Table 4) to assess possible patterns in the results. Eleven studies including 10 species satisfied our criteria. These 11 studies provide a somewhat different picture of juvenile survival than those in the unfiltered collection. In the high-quality subset, weight is a predictor of juvenile survival in nine cases, and not associated with survival in only one (Table 2B), but in the unfiltered collection the respective totals are 40 and 34 (Table 2A). In both summaries, the body-reserve advantage hypothesis receives strong support from the studies in which a weight effect was detected (weight and juvenile survival were positively correlated), but only the high-quality subset suggests that this pattern is general in birds (only one study found no association). Both data sets suggest that large size and early breeding sometimes, but not nearly always, promotes juvenile survival, and that cohort and sex effects are often important but are not ubiquitous. The high-quality subset has too few results for effects of size, clutch-brood size, hatching order-brood rank, and growth rate to make any inference. In fact, the sample size of 11 across all major clades highlights the need for many more studies that avoid the pitfalls that distinguish the unfiltered and filtered summaries. We especially need studies outside the Passeriformes (Table 2B); even the support for the

TABLE 2. Taxonomic summary for studies on the relationship between postfledging survival and several variables. (A) Summary of all studies in Table 1. (B) Summary of those that met the 11 criteria outlined in the text. Key: “+” = positive relationship, except in the case of year and sex, where “+” indicates that a relationship was found; “-” = negative relationship; “0” = no relationship; and “U” = parameter not examined, results of multiple studies inconclusive, or not applicable to the species in question (e.g., clutch size in Procellariiformes). Taxonomy follows Ericson et al. (2006), Hackett et al. (2008), and Chesser et al. 2010.

A.

Order	Species ( <i>n</i> )	Weight				Size				Timing				Clutch- brood size				Hatching order- brood rank				Growth rate				Cohort			Sex			
		+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	0	U	+	0	U	
Galliformes	1			1				1				1				1				1						1				1		
Anseriformes	10	4		4	2	1			9		6	1	3	2	1	7			10			10	5	2	3			3		7		
Columbiformes	2			1	1				2				2			2			2		1	1		1	1		1		1			
Cuculiformes	1	1							1				1			1			1		1			1						1		
Gruiformes	3	1		1	1	1			2		1		2		1	2			3			3	2		1	1	1	1	1			
Procellariiformes	4	3	1	1	1	1			2	2	1	3	1		4			4		2	4	1		3			3		4			
Water Bird Sphenisciformes	4	1		1	2				4		2		2	1	3			3		1	3		4	2		2	1		3			
Bird Clade Ciconiiformes	1			1					1				1		1			1		1	1						1					
Clade Pelecaniformes	1				1				1				1		1			1		1	1								1			
Suliformes	3	2			1	1			2		3			1	2			3	1		2	1	1	1	1	1	1	1	2			
Charadriiformes	16	4		7	5	2			1	13	1	6	5	4	2	1	13	2		14	2	3	11	5		11		1	1	15		
Coraciiformes	2	2							1	1		1	1				2			2		2				2		2				
Land Bird Strigiformes	2				2				2		1	1		1	1			2		2		2				2		1	1			
Bird Clade Accipitriformes	3	1		2					3		1	2			2	1		3		1	2		2	1	1	1	1	1	1			
Clade Falconiformes	1			1					1				1		1			1		1		1					1					
Passeriformes	41	21	1	14	7	8			10	24	2	13	13	15	3	5	15	19	2	2	38	5	37	13	12	17	5	8	28			
Total	95	40	2	34	22	14	0	14	69	3	33	26	36	9	7	21	59	0	4	4	88	3	0	12	83	31	19	46	10	19	66	

B.

Order	Species ( <i>n</i> )	Weight				Size				Timing				Clutch- brood size				Hatching order- brood rank				Growth rate				Cohort			Sex		
		+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	0	U	+	0	U
Anseriformes	1	1						1			1				1			1		1	1									1	
Gruiformes	1	1						1				1						1		1	1							1			
Water Bird Sphenisciformes	1	1						1				1						1		1	1							1			
Clade Suliformes	1	1					1				1				1			1	1					1				1			
Charadriiformes	1	1						1				1						1		1	1							1			
Land Bird Clade Accipitriformes	1			1				1			1				1			1		1		1					1				
Bird Clade Passeriformes	4	4						4		3	1			1	3			4		4	1	2	1	2	2	2	2	2	2		
Total	10	9	0	1	0	1	0	0	9	0	5	2	3	0	0	2	8	0	0	0	10	1	0	0	9	5	4	1	5	4	1

TABLE 3. Summary of studies on the relationship between postfledging survival (i.e., annual adult survival probability, or species longevity; see Table S2 in the online supplement) and several variables. (A) Summary of all studies in Table 1. (B) Summary of those that met the 11 criteria outlined in the text. Key: “+” = positive relationship, except in the case of year and sex, where “+” indicates that a relationship was found; “-” = negative relationship; “0” = no relationship; and “U” = parameter not examined, results of multiple studies inconclusive, or not applicable to the species in question. t

A.

Annual adult survival probability	Species (n)	Mass				Size				Timing				Clutch-brood size				Hatching order-brood rank				Growth rate				Cohort			Sex		
		+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	0	U	+	0	U
$x \leq 0.6$	25	9		11	5	5		4	16	1	10	7	7	2	1	9	13					25		1	24	10	7	8	3	5	17
$0.6 < x \leq 0.8$	34	16	1	10	9	4		6	25	2	10	8	16	3	5	9	18		2	3	30		5	30	9	7	19	3	5	26	
$0.8 < x \leq 0.87$	8	4		3	1				8	2	3	3	1			2	5			1	7		8	1	3	4	1	3	4		
$x > 0.87$	28	11	1	10	7	5		4	20		11	8	10	3	1	1	23		2		26	3	6	21	11	2	15	3	6	19	
Total	95	40	2	34	22	14	0	14	69	3	33	26	36	9	7	21	59	0	4	4	88	3	0	12	83	31	19	46	10	19	66

B.

Annual adult survival probability	Species (n)	Mass				Size				Timing				Clutch-brood size				Hatching order-brood rank				Growth rate				Cohort			Sex		
		+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	0	U	+	0	U
$x \leq 0.6$	1	1						1				1					1					1				1	1			1	
$0.6 < x \leq 0.8$	3	3						3		2	1					1	2				3			3			2	1	1	2	
$0.8 < x \leq 0.87$	0																														
$x > 0.87$	6	5		1		1			5	2	1	3				1	5				6	1			5	4	2		3	2	1
Total	10	9	0	1	0	1	0	0	9	0	5	2	3	0	0	2	8	0	0	0	10	1	0	0	9	5	4	1	5	4	1



TABLE 4. Summary of studies on the relationship between postfledging survival and several variables by developmental mode (see Table S2 in online supplement). (A) Summary of all studies in Table 1. (B) Summary of those that met the 11 criteria outlined in the text. Key: "+" = positive relationship, except in the case of year and sex, where "+" indicates that a relationship was found; "-" = negative relationship; "0" = no relationship; and "U" = parameter not examined, results of multiple studies inconclusive, or not applicable to the species in question.

## A.

Developmental mode	Species (n)	Mass				Size				Timing				Clutch-brood size				Hatching order-brood rank				Growth rate				Cohort			Sex		
		+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	0	U	+	0	U
Precocial	15	6		7	2	1		1	13	1	7	2	5	2		2	11			15			1	14	6	2	7	1	4	10	
Semi-precocial	23	7	1	8	8	3		2	19		9	7	8	3	1		19	2	2	20	2		4	18	9		14	1	1	21	
Altricial	57	27	1	19	12	10		11	37	2	17	17	23	4	6	19	29	2	2		1		7		16	17	25	8	14	35	
Total	95	40	2	34	22	14	0	14	69	3	33	26	36	9	7	21	59	0	4	4	35	3	0	12	32	31	19	46	10	19	66

## B.

Developmental mode	Species (n)	Mass				Size				Timing				Clutch-brood size				Hatching order-brood rank				Growth rate				Cohort			Sex		
		+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	-	0	U	+	0	U	+	0	U
Precocial	2	2							2		1		1			1	1			2			2	2					1		1
Semi-precocial	2	2							2			1	1				2			2			2	2					1	1	
Altricial	6	5		1		1			5		4	1	1			1	5			6	1		5	1	4	1	3	3			
Total	10	9	0	1	0	1	0	0	9	0	5	2	3	0	0	2	8	0	0	0	10	1	0	0	9	5	4	1	5	4	1

body-reserve advantage hypothesis from Table 2B is effectively a passeriform result.

Summaries arranged by life span (Table 3) suggest similar observations. The longest-lived species appear to exhibit a stronger cohort effect than shorter-lived species in the unfiltered summary (Table 3A), as would be predicted by life-history considerations of parents observing a ceiling on reproductive effort (Goodman 1974, Mauck and Grubb 1995). During poor breeding conditions, poor-quality offspring would be produced by members of long-lived species, and these offspring would have poor juvenile survival, leading to a cohort effect. This effect is absent in the high-quality subset (Table 3B), but we suggest that we cannot evaluate this life-history prediction with confidence given the meager high-quality data and the problems of interpretation inherent in the unfiltered data set. Table 3A provokes some interest in a weaker sex effect among the longest-lived species than among others, but too few high-quality studies exist to conclude anything.

The opportunity for parents to influence the juvenile survival of their offspring may be higher for species with more altricial development than more precocial development, if the reproductive effort per offspring increases as altriciality increases. Shortfalls in parental effort might be manifested more in poor juvenile survival in more altricial taxa as a result. Alternatively, altricial parents may be better able to buffer poor rearing conditions via their more extended parental effort. The unfiltered data set provides little support for either of these ideas, with the exception of the cohort effect (Table 4A). Among the unfiltered studies, altricials appear to exhibit a weaker cohort effect than semi-precocials and precocials. The high-quality subset (Table 4B) is too sparse to draw a conclusion regarding the cohort effect (or any other effect). We have a palette of important questions to answer regarding juvenile survival in birds, but few easily interpretable results to answer those questions.

*Juvenile survival in Nazca Boobies.*—We addressed these issues in a study of sex-specific juvenile survival in a seabird, the Nazca Booby (*Sula granti*). This species exhibits high natal philopatry (essentially 100%; Huyvaert and Anderson 2004), long life span (Anderson and Apanius 2003), and high encounter probabilities of adults in our annual band-resight surveys, removing a common source of bias in survival estimates of other species. Our earlier CMR model (Maness and Anderson 2007) of annual adult survival gave high average resight

probabilities for breeding males (0.994), breeding females (0.993), nonbreeding males (0.918), and nonbreeding females (0.896). Consider the logistically challenging life history of a female that appears in the colony as an adult at the typical age (4 years, see below) and dies young (age 8) without breeding: the probability that she will never be seen as an adult, and considered to have died during the juvenile period, is only  $(1 - 0.896)^4 = 0.0001$ . Sibling competition in multi-chick broods is an uncontrolled effect on development in many studies of the effects of parental care on juvenile survival. Nazca Boobies raise only a single offspring per annual breeding season (Humphries et al. 2006) from a clutch of one or two eggs (Anderson 1990). If two eggs hatch, only one nestling (usually the product of the first egg) survives siblicidal interactions that typically cause brood reduction before the nestling's fifth day (Anderson 1989, Humphries et al. 2006), so sibling competition is ephemeral (usually <3% of the 158-day average period of offspring dependence; Humphries et al. 2006, Maness et al. 2011). As a consequence, brood size does not affect the duration of nestling development or morphological measures around the time of fledging (Humphries et al. 2006; however, behavioral effects in adulthood have been suggested; Müller et al. 2011), and sibling competition should not obscure other influences on survival.

Considering all 3,435 sexed fledglings with morphological measures taken at the 1% down stage (see below) in our study, females were the larger and heavier sex when they attained juvenal plumage (culmen length: females, mean  $\pm$  SD =  $103.9 \pm 2.7$  mm; males,  $100.9 \pm 2.6$  mm; weight: females,  $1,877 \pm 260$  g; males,  $1,699 \pm 225$  g;  $n = 1,594$  females and 1,841 males; T. J. Maness and D. J. Anderson unpubl. data). This size difference of 10.5% is similar to that in a separate study (11.1%), whereas the parents of those fledglings differed by 13.0%, with absolute weights varying according to a number of factors (for details, see Apanius et al. 2008). Several lines of evidence indicate that parents satisfy the food demand of daughters less often than that of sons (Anderson et al. 1993, Townsend et al. 2007, Apanius et al. 2008). Consistent with this result, Maness et al. (2007) used data from two cohorts to conclude that male Nazca Boobies survive the period between fledging and appearing in the colony as an adult (Fig. 1) at a higher rate than females, contributing to the development of a consistently male-biased adult sex ratio (Townsend and Anderson 2007a). Females

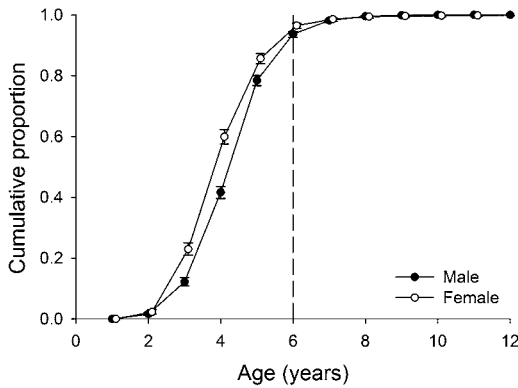


FIG. 1. Age of first appearance in the breeding colony as adults for male and female Nazca Boobies from 16 cohorts (1984–1985 to 1987–1988, and 1992–1993 to 2003–2004). Brackets show 95% confidence intervals. Dashed line represents the age of the youngest cohort used in our analyses.

should be expected to survive better than males under both the body-reserve advantage and the size advantage hypotheses, but they do not. Nonetheless, the weight or size advantage might still operate within sex if the sex difference in survival is unrelated to size or weight differences. Here, we evaluate the high weight–high survival prediction within and between sexes, as well as the relationship of juvenile survival to several other indicators of the nestling experience: size independent of weight, age at which the nestling attained juvenal plumage, hatching date, and clutch size (which appears to reflect general parental ability; Clifford and Anderson 2001b, Townsend and Anderson 2007b). Temporally variable conditions are likely to influence juvenile survival, so we also examined the effect of cohort on juvenile survival.

We followed the fates of 2,631 Nazca Boobies from seven cohorts, sexed by molecular means and providing extensive data on their nestling experience, making this the largest study of sex-specific juvenile survival to date for any bird. To determine the sex ratios at fledging and upon reaching adulthood, we sexed 5,196 nestlings from the same seven cohorts and followed them to adulthood. This larger group of birds contained individuals from unmonitored nests (described below) and could not be included in the analysis of juvenile survival that included the monitored predictors described above. The large sample size permits the use of path analysis, not used in most previous studies (but see Blums et al. 2002).

## STUDY SITE AND METHODS

*Terminology.*—We construe the motivation of this area of research as an effort to explain variation in the survival probability of newly independent individuals, especially using aspects of life during the period of dependence on parents as predictors. After leaving the nest, young birds are difficult to monitor, and particularly to capture and measure, leading many investigators to use the last measurements available before permanent nest-leaving as proxies for those measurements at the end of parental care. Frequently this practice can be justified, especially if parental care ends at nest-leaving. Parental care *after* nest-leaving might interact with, or override, the effect of condition at nest-leaving on survival after the end of parental care, so clear terminology regarding the timing of offspring measurement in relation to the timing of the end of parental care is helpful. Similarly, “fledging” can be used to indicate permanent nest-leaving, taking flight for the first time, or reaching the end of parental care, but these events may occur at different ages: precocial species may leave the nest permanently long before the first flight, and altricial species may leave the nest for the last time long after taking the first flight.

Throughout this monograph, we will use “fledging” to refer to taking flight for the first time, “fledgling” to refer to a dependent bird that can fly, and “juvenile” to refer to a bird no longer receiving parental care but not yet adult. By “nest-leaving,” we mean the final departure from the natal nest (approximately coincident with becoming a juvenile in Nazca Boobies; Maness et al. 2011). The operational definition of the end of the juvenile period will be taxon specific and might involve attaining adult plumage or attending a breeding site. In our field study, we treat the period between the end of parental care and the subsequent appearance in the breeding colony some years later (virtually always in adult plumage) as the “juvenile” period, and the probability of survival from the beginning of that period to the end as “juvenile survival.”

Our dependent variable is “survival to adulthood” in two of our analyses (path analysis and logistic regression). By this we mean survival across the entire period from the end of parental care until the bird appears as a functional adult, in adult plumage, in the breeding colony. We distinguish this from age-dependent survival during this period, which is not a dependent variable in our study. Survival to adulthood is a

dichotomous variable: a bird either survived this period of variable length (Fig. 1) or did not. In a CMR analysis, we used a multistate model with recapture histories represented as three possible states in a given year: An unobservable juvenile state (J), an adult state ("A"), and "0" for a bird that could be observed but was not seen in the colony. We used the dichotomous outcome variable (survived to appear in the colony as adult or died) to test the prediction derived from the CMR model equation.

*Field techniques.*—Our group has conducted long-term demographic studies on a population of Nazca Boobies at Punta Cevallos, Isla Española, Galápagos Islands (1°23'S, 89°37'W), Ecuador, since 1984. The study site comprises three subcolonies, detailed in Huyvaert and Anderson (2004) and Apanius et al. (2008). Breeding seasons include parts of two calendar years; most eggs are laid between October and January, and most young fledge by June of the following year. Beginning in the 1992–1993 breeding season, all nests in the study site with at least one banded parent were monitored daily (for details, see Apanius et al. 2008) from the date of clutch initiation until the nestling attained juvenal plumage or the reproductive attempt failed. Nests with two unbanded parents were "unmonitored," except within a subsection of subcolony 1 known as the "Study Area" (Apanius et al. 2008), in which all nests were monitored. Volant offspring in juvenal plumage leave the nest for increasingly longer periods each day, making difficult the determination of the actual date of permanent nest-leaving. Growth is virtually complete in offspring when they attain juvenal plumage, although parental care continues beyond this point (Apanius et al. 2008, Maness et al. 2011), so we assessed a nestling's weight and structural size at the end of parental care with data collected at the "1% down" developmental timepoint (when 99% of the nestling's down has been replaced by pennaceous juvenal plumage). Nestlings reach the 1% down stage at a mean ( $\pm$  SD) age of  $100.9 \pm 8.8$  days after hatching (Humphries et al. 2006), and take their first flight to the sea (indicated by the sudden absence of guano on their feet) approximately  $12.0 \pm 5.4$  days later (Maness et al. 2011). Offspring then leave the colony, on average,  $45.3 \pm 10.0$  days after their first flight to the sea. During the 3 days before the offspring's departure, parents do not attend the colony, which apparently triggers the offspring's departure from it (Maness et al. 2011). Ages at first flight and at departure

from the colony are highly correlated with age at the 1% down stage (Humphries et al. 2006, Apanius et al. 2008), and little mortality occurs between the 1% down point and departure from the colony (Humphries et al. 2006, Maness et al. 2007, Maness et al. 2011). These circumstances justify the use of status (values of our predictor variables) at the 1% down stage as a proxy for status at permanent nest-leaving and the end of parental care. Nestlings at the 1% down stage have nearly fledged, so for convenience we refer to them as "fledglings." In most breeding seasons, we banded all fledglings from monitored and unmonitored nests. Fourteen birds that died between reaching the 1% down stage and taking their first flight to the sea were excluded from all analyses, because these birds did not reach independence.

Juveniles vacate the Punta Cevallos colony for several years, and band returns indicate that they live at sea off the Central American and Mexican Pacific coasts (Huyvaert and Anderson 2004). After attaining adult plumage, virtually all survivors return to Punta Cevallos and become permanent residents. The "age of first return" indicates the first sighting of a young adult in the colony in annual band-resight surveys (Huyvaert and Anderson 2004) or in nest monitoring of breeders (Huyvaert and Anderson 2004, Apanius et al. 2008). To identify cohorts to include in our survival analysis, we determined the distribution of ages of first return for members of each cohort. To ensure essentially comprehensive coverage of surviving birds returning to the colony, the cohorts in the analysis all had at least 1 year pass (after peak return age) with  $\leq 7$  new individuals making first appearances during the year of our analysis. The four fledgling cohorts between 1984–1985 and 1987–1988 and the 12 cohorts between 1992–1993 and 2003–2004 (no young were banded from the 1988–1989 season to the 1991–1992 season) satisfied this criterion (Table 5). Most (94.9%; Fig. 1) surviving birds first return to the breeding colony within 6 years of vacating it, and essentially all (99.97%; Fig. 1) return by age 12, so almost all surviving offspring from the 1998–1999 to 2004–2005 cohorts that will ever return as adults should have returned at the time of our analyses (2011), when the youngest subject birds were 6 years and the oldest birds were 12 years old. We did not conduct a band-resight survey in 1988–1989, and individuals from earlier cohorts that appeared for the first time that season would be attributed to older age classes; therefore, our estimates of age of first appearance here are

TABLE 5. Age at which individual (A) male and (B) female fledglings banded in 16 cohorts first appeared in the colony as adults ( $n$  = total number seen). No birds were banded during 1988–1991, and no survey was conducted in 1988–1989 ( $na$  = “not applicable” because individuals had not reached that age by the 2010–2011 band-resight survey, and  $na$  = “not applicable” for some younger ages of the oldest cohorts).

## A.

Cohort	$n$	Males: Age first seen (years)																
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1984–85	27	2	13	na	7	1	2	1	1	0	0	0	0	0	0	0	0	0
1985–86	71	11	na	31	15	4	5	4	1	0	0	0	0	0	0	0	0	0
1986–87	99	na	34	46	9	6	3	1	0	0	0	0	0	0	0	0	0	0
1987–88	139	8	47	37	34	5	3	2	2	1	0	0	0	0	0	0	0	0
1992–93	187	1	5	85	58	28	6	1	3	0	0	0	0	0	0	0	0	0
1993–94	93	0	11	29	37	7	6	3	0	0	0	0	0	0	0	0	0	na
1994–95	191	0	16	102	38	25	9	1	0	0	0	0	0	0	0	0	na	na
1995–96	130	0	14	25	58	12	15	5	0	1	0	0	0	0	0	na	na	na
1996–97	86	1	3	23	27	31	1	0	0	0	0	0	0	0	na	na	na	na
1997–98	0	0	0	0	0	0	0	0	0	0	0	0	0	na	na	na	na	na
1998–99	71	0	8	20	30	10	2	1	0	0	0	0	na	na	na	na	na	na
1999–00	4	0	0	1	2	1	0	0	0	0	0	na	na	na	na	na	na	na
2000–01	214	0	9	51	94	29	20	10	1	0	na	na	na	na	na	na	na	na
2001–02	171	1	3	56	51	45	14	1	0	na	na	na	na	na	na	na	na	na
2002–03	529	0	69	87	227	131	13	2	na	na	na	na	na	na	na	na	na	na
2003–04	307	12	14	90	168	18	5	na	na	na	na	na	na	na	na	na	na	na
Total	2,319	36	246	683	855	353	104	32	8	2	0	0	0	0	0	0	0	0

## B.

Cohort	$n$	Females: Age first seen (years)																
		2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
1984–85	36	1	19	na	8	2	3	0	0	0	1	1	1	0	0	0	0	0
1985–86	53	11	na	22	12	5	2	0	0	0	0	1	0	0	0	0	0	0
1986–87	58	na	17	29	6	3	1	0	0	2	0	0	0	0	0	0	0	0
1987–88	104	5	54	29	8	7	0	1	0	0	0	0	0	0	0	0	0	0
1992–93	128	0	6	92	16	11	1	2	0	0	0	0	0	0	0	0	0	0
1993–94	78	1	22	24	26	2	1	2	0	0	0	0	0	0	0	0	0	na
1994–95	118	1	12	69	19	12	1	3	1	0	0	0	0	0	0	0	na	na
1995–96	116	0	23	32	42	16	3	0	0	0	0	0	0	0	0	na	na	na
1996–97	58	0	5	38	11	4	0	0	0	0	0	0	0	0	na	na	na	na
1997–98	0	0	0	0	0	0	0	0	0	0	0	0	0	na	na	na	na	na
1998–99	49	0	11	25	9	1	1	2	0	0	0	0	na	na	na	na	na	na
1999–00	1	0	0	0	0	1	0	0	0	0	0	na	na	na	na	na	na	na
2000–01	112	3	15	50	31	6	7	0	0	0	na	na	na	na	na	na	na	na
2001–02	111	0	13	43	24	22	5	2	2	na	na	na	na	na	na	na	na	na
2002–03	427	8	118	88	124	80	7	2	na	na	na	na	na	na	na	na	na	na
2003–04	195	7	25	67	88	6	2	na	na	na	na	na	na	na	na	na	na	na
Total	1,644	37	340	608	424	178	34	14	3	2	1	2	1	0	0	0	0	0

marginally conservative, with the gain in sample size overbalancing this effect.

For molecular sexing, we collected feather samples from all fledglings during the 1998–1999

through the 2000–2001 breeding seasons and blood samples during the 2001–2002, 2002–2003, 2003–2004, and 2004–2005 breeding seasons. Feathers were preserved dry in plastic bags or

in vials containing 70% EtOH. Blood samples were collected by brachial venipuncture onto a filter paper tab and preserved in 70% EtOH. We followed a modified polymerase chain reaction (PCR) protocol of Fridolfsson and Ellegren (1999). Details of DNA extraction, the PCR protocol, and validation of the technique are provided in Maness et al. (2007) and Apanius et al. (2008). Maness et al. (2007) demonstrated 100% accuracy of this technique for this species. In the present study, we ground-truthed the PCR sexes using sex-specific voices (Nelson 1978) with birds that provided both PCR sex and adult voice (see below).

For the study of juvenile survival, we used sexed fledglings from the seven cohorts 1998–1999 to 2004–2005, on the basis of the reasoning above. We considered fledglings from these cohorts to have survived to adulthood if they were observed at least once, either during an annual band-resight survey or as a breeder. Our only use of data from the unmonitored nests was in combination with data from monitored nests to calculate fledging and return sex ratios at the population level. We express sex ratio as the proportion of the population that is male. A total of 2,676 males and 2,486 females contributed to calculation of the fledging sex ratio, 1,546 males and 1,078 females to the return sex ratio, and 1,348 males and 1,283 females to the survival analyses.

*Statistical analysis.*—We used path analyses in AMOS, version 19.0.0 (SPSS, Chicago, Illinois), to evaluate predictors of juvenile survival. Path analysis is an extension of the regression model. A path coefficient is a standardized regression coefficient (beta) showing the direct effect of an independent variable on a dependent variable in the path model. When the model has two or more independent (equivalent to “exogenous” in this case) variables, path coefficients are partial regression coefficients that measure the extent of the effect of one variable on another in the path model while controlling other prior variables. The regression weights predicted by the model are compared with the observed correlation matrix for the variables, and a goodness-of-fit statistic and residual sums of squares are calculated. The correct correlation matrix must be used in path analyses. In the case of correlated exogenous interval variables, the path is equivalent to a Pearson correlation. Polychoric correlation is used for two ordinal variables, polyserial for interval and an ordinal, biserial for an interval and a dichotomy, and tetrachoric for two dichotomies. For example, biserial correlation allows calculation of correlation between sex (a

dichotomy) and wing length (an interval); a positive correlation in this case would indicate that the sex ratio of a cohort is more female-biased if that cohort tends to have a long wing length (see below). AMOS can accommodate dichotomous and ordinal variables through Bayesian estimation using a Markov-chain Monte Carlo algorithm. The dependent variable of our analysis is dichotomous (0 = did not survive, 1 = survived to be seen as an adult); AMOS uses a probit link for dichotomous outcome variables. Another assumption of path analysis is that the same sample (i.e., no missing values) is required for all regressions in the model. Large sample sizes, at least 10× and ideally 20× as many cases as parameters (Kline 1998), are required to assess significance and fit of models adequately.

We expected a path analysis to perform better than other statistical approaches for several reasons (see above). To evaluate this expectation, we modeled juvenile survival with path analysis, CMR, logistic regression, and analysis of variance (ANOVA) with the same data set of predictors and compared their performances. The predictors (weight, age at fledging, and others) are correlated, so CMR and other regression approaches should have problems with inflated error in parameter estimation. We used all predictors in all modeling approaches to fairly compare performance with use of correlated predictors. Path analysis allows us to examine the relative importance of multiple related predictors of juvenile survival in a single model, a particular advantage that we emphasize in this monograph.

CMR techniques are also used to determine recapture probabilities; in our system, the recapture probabilities of juvenile survivors approach 100% because natal philopatry is essentially 100% (Huyvaert and Anderson 2004) and our encounter probabilities are high (see above). To compare CMR with path analysis, we estimated juvenile survival using Program MARK (White and Burnham 1999). Candidate models included survival (S) probability and resight (p) probability parameters, offspring sex as a grouping variable, an unobservable J state, an A state, and the seven predictor variables described in detail below. Juvenile Nazca Boobies are absent from the study colony and unavailable for recapture for  $\geq 1$  year, and most return around the age of 4 years (Fig. 1). Survival during the juvenile (S:J) period was limited to the 2 years after fledging, and survival after the second year was assumed to be the same as the survival in the A state (S:A), as

has been assumed in other species with delayed maturity (e.g., Bailey et al. 2010). S:J could remain constant ( $\cdot$ ), or vary by year (t), offspring sex (sex), cohort (c), and by the predictors described below. S:A included a sex effect; resight probability of adults (p:A) included sex and age effects (determined by modeling age-specific survival of adults; T. J. Maness and D. J. Anderson unpubl. data). Transition probability between the J and A states (Psi:J-A) included sex and age effects (determined by modeling age-specific survival of adults; T. J. Maness and D. J. Anderson unpubl. data). We used Akaike's information criterion (AIC) for model selection and ranking (Burnham and Anderson 2002). In practice, we used QAIC<sub>c</sub>, a version of AIC incorporating adjustment of the variance inflation factor, based on an estimate of median  $\hat{c}$  (White 2002). Models with the lowest QAIC<sub>c</sub> values were assumed to better explain variation in the data. The median  $\hat{c}$  procedure cannot be performed on a model with individual covariates, so we estimated median  $\hat{c}$  using a simplified input file that did not include covariates.

We also compared the outcome of our path analysis with logistic regression using nested, forward stepwise, and backward stepwise techniques. We predicted that the path analysis would perform better than these techniques because the correlation between predictors would impede the performance of a multifactorial logistic regression and the separate-models technique would have low power. Path analysis uses a probit link function, and CMR and logistic regression use a logit link function, to predict which group (in our case, survivor or nonsurvivor) an individual should belong to, based on the associated model of dependent and predictor variables. We derived such predictions for each fledgling from each of the three modeling approaches and compared each bird's predicted group with its actual postfledging survival or mortality. To compare the performance of the three modeling approaches, we used the percentage of birds classified correctly, a likelihood version of  $R^2$  (Anderson 2008), the complexity of the models, and the unconditional variance associated with parameter estimation (see equation in Anderson 2008:111) from each modeling approach.

Some researchers have used individual ANOVAs ( $t$ -tests) to assess predictors of juvenile survival (e.g., Weimerskirch et al. 2000). We cannot compare the performance of these tests with our other statistical approaches because the logical direction of these tests is reversed, in that all other approaches attempt to predict which group

(survivor or nonsurvivor) a bird will fall into given its particular set of measurements, whereas the ANOVA approach categorizes birds in groups based on known survivor–nonsurvivor status, then ascertains whether differences exist in their measurements (reversing the direction of the test from prospective to retrospective). We rank individual tests using  $F$  ratios and  $P$  values because information-theory approaches cannot be used to rank ANOVAs when the outcome variables are different.

All statistical analyses, except the path analysis and CMR, were performed with SPSS unless we state otherwise.

*Parameter conditioning.*—We used the following predictors of juvenile survival, measured on the day that a nestling reached the 1% down stage (and so approximately “fledgling” status): weight (g), culmen length (mm), wing length (mm), age at fledging (days), hatching date (see below), clutch–brood effect (see below), cohort (encompassing effect of breeding year), and sex. We also tested the quadratic of weight, culmen length, wing length, age at fledging, and hatching date to examine the possibility that these predictors are subject to stabilizing (or disruptive) selection (e.g., stabilizing selection on body size in Sociable Weavers; Covas et al. 2002). We examined saturated models initially, in which all predictor variables could correlate freely. We then reduced the models and used AIC<sub>c</sub> (adjusted for small sample sizes) following Burnham and Anderson (2002) to select the best-performing model(s). We did not use tarsus length as a predictor because it was difficult to measure consistently.

Hatching date (HD) was expressed in a 2-year Julian calendar format. Nazca Boobies breed seasonally at Punta Cevallos from October to June. Our calendar starts on 1 January of the year in which a given breeding season begins and extends to the end of that season in the following year. For example, one nestling in the 2000–2001 breeding season fledged on day 491 (5 May 2001) from an egg laid on day 334 (29 November 2000) and hatched on day 376 (10 January 2001). Laying date and HD expressed the same information (Pearson  $r = 0.97$ ), so we used only HD in our analyses. HD was standardized ( $z$ -score) within breeding season to control between-season differences in mean and variance in HD.

We considered two proxies for environmental quality of a given breeding season: the number of breeding attempts and the number of young reaching the 1% down stage, both in an area in which

every nest is monitored. The number of attempts is relatively constant across years, whereas production of fledglings varies substantially (Maness et al. 2007), which suggests significant unpredictable variation in environmental quality after egg laying. We used the number of young reaching the 1% down stage as our proxy, reasoning that it captured that unpredictable variation during the actual breeding season, when offspring attributes were developed. For most seasons of the study, we assessed fledging success with banding records, because we banded all fledglings at our site in those seasons. In 2003–2004 only, we banded all fledglings from monitored nests (see above), but not all unmonitored fledglings, because of a shortage of bands in the field. In that season, we marked and determined the GPS location of all unmonitored nests as part of another study, so we know the number of unmonitored nests initiated in that season. To estimate the total number of fledglings produced by these unbanded parents, we multiplied the total number of unmonitored nests initiated (1,270) by the fledging probability determined from monitored nests that season; this estimate matched the proportion represented by unmonitored fledglings produced in other cohorts (Table 6). Unmonitored fledglings were not used in our path analyses, so this group of unbanded fledglings from 2003–2004 did not influence our models. However, these unbanded fledglings could have biased our estimate of fledging sex ratio for this cohort, because we banded the first 273 unmonitored chicks that fledged in 2003–2004 and did not band the ~387 chicks that fledged later

in the season. If offspring sex ratio differs between the early- and late-season breeders, our estimate of fledging sex ratio will be biased toward the early-season breeder's preferred offspring sex. However, no trend with breeding-season date was found for hatching or fledging sex ratios in an earlier study (Maness et al. 2007).

We used weight and two size measures (culmen and wing lengths) separately in our analyses. Many studies have combined weight and linear measures in a body condition index (BCI; usually weight corrected for body size; reviewed in Brown 1996). Individuals with greater weight for their body size (high BCI) are assumed to have greater energy reserves than individuals with lower weight for their body size (low BCI; reviewed in Brown 1996). Principal component analysis (PCA) of linear body measurements can be used to summarize structural size using correlated variables (Rising and Somers 1989, Brown 1996), and the first principal component is used to calculate a BCI. Recently, the methods used to calculate BCIs have generated much controversy, and theoretical models indicate that the relationship between body weight and condition indices may be difficult to interpret (Brown 1996, Jakob et al. 1996, Green 2001, Schulte-Hostedde et al. 2005, Schamber et al. 2009). In our approach, we can determine the separate direct effects of size and weight on juvenile survival because the path analysis will incorporate the correlations between these measures. Because BCIs statistically remove the effect of body size from body weight, studies using this

TABLE 6. Number of fledglings banded in the colony, cohort size (i.e., number of fledglings produced at the study site by both banded and unbanded parents; see text), number of fledglings that survived to adulthood, probability of a nest producing a fledging, number of banded fledglings that provided a tissue sample, number of tissue-sampled fledglings sexed by polymerase chain reaction (PCR), proportion of tissue-sampled fledglings sexed by PCR, and number of individuals whose PCR and adult sex did not match in each cohort.

Cohort	Number of fledglings banded	Cohort size ( <i>n</i> survived)	Proportion of nests producing a fledgling	Number of banded fledglings with tissue sample	Number of fledglings sexed by PCR	Proportion sexed by PCR	Mismatched PCR and adult sex
1998–99	486	486 (122)	0.31	427	324	0.76	1
1999–00	25	25 (5)	0.03	25	21	0.84	0
2000–01	856	856 (325)	0.34	783	752	0.96	1
2001–02	629	629 (280)	0.23	625	610	0.98	1
2002–03	1,670	1,670 (958)	0.62	1,670	1,587	0.95	4
2003–04	934	1,321 (502)	0.52	829	805	0.97	0
2004–05	1,124	1,124 (662)	0.53	1,097	1,068	0.97	2



technique cannot assess the independent effects of these two morphological measures on a dependent variable. The ability of path analysis to avoid problems associated with BCIs is a major advantage of the path analysis approach.

Nestlings' weight-specific growth can be flexible but generally follows a sigmoid trajectory (Ricklefs 1968, Starck and Ricklefs 1998). The asymptotic weight (reached around the time of fledging) often exceeds adult weight, may show yearly variation related to environmental conditions, and can differ by sex, particularly in sexually size-dimorphic species (Starck and Ricklefs 1998). Parents may satisfy the sex-specific food requirement of offspring of one sex more completely than that of the other (reviewed in Anderson et al. 1993, Townsend et al. 2007). In poor breeding seasons, the needs of the larger sex may not be met as well as those of the smaller sex, particularly if parents invest equally in each individual, regardless of sex (Anderson et al. 1993, Townsend et al. 2007). We have seen this pattern in Nazca Boobies: female adults are larger, and female nestlings achieve their growth potential less often, than males (Townsend et al. 2007, Apanius et al. 2008). To avoid problems associated with an absolute measure, fledgling weight could be rescaled by comparison with a sex-specific adult target weight, but this may not account for different sex-specific asymptotic weight targets: one sex may need only to reach a target that is 1.2× the adult weight, whereas the other may need to reach a target that is 1.4× the adult weight. Fledgling weight can also be rescaled by calculating the residual that results from subtraction of an individual's weight from the sex-specific mean

weight of all fledglings (e.g., Phillips and Furness 1998). However, if one sex's food requirement is more completely satisfied than that of the other sex, this rescaling method is as inadequate as the comparison of adults described above.

Recognizing these issues, we calculated target weights by a new method that uses our long-term database. First, we calculated the mean fledgling weight of all males and, separately, all females that survived the juvenile period from the Study Area for 10 cohorts (all cohorts with enough time for ≥99.0% of survivors to have returned to the colony as adults) beginning with the 1992–1993 breeding season. Because we have monitored all nests in the Study Area in all years since 1992–1993, this method characterizes fledging weight at the population level in an unbiased manner. The 1995–1996 breeding season had the highest survival probability of all cohorts examined (Table 7), so we used the mean fledgling weights of male and female survivors from this season as our best indicator of the optimal fledgling weight ("target weight"). With a value of target weight as a reference, we then rescaled each fledgling's (1998–1999 to 2004–2005 cohorts) weight by subtracting its weight from its sex's target weight. The sign and magnitude of this "target weight score" indicated how closely a bird approached its sex-specific target weight. For example, if a female fledgling's weight was 1,900 g, her target weight score (TWS) was  $1,900 - 2,047.7 = -147.7$  g. These TWSs were used as a predictor in the modeling.

Nazca Boobies raise single-offspring broods (Humphries et al. 2006) from a clutch of one or two eggs (Anderson 1990). The second egg in

TABLE 7. Probability of surviving the juvenile period at sea for fledgling Nazca Boobies from an area of the colony known as the "Study Area," and the sex-specific fledging masses of survivors (CI = confidence interval; na = not applicable because no fledglings survived). The 1995–1996 cohort is in bold to indicate that the probability of survival was highest for that group (see text).

Cohort	Proportion surviving (95% CI)	Mean fledgling weight (g) of female survivors (95% CI)	Mean fledgling weight (g) of male survivors (95% CI)
1992–93	0.41 (0.33–0.49)	2,008.8 (1,840.2–2,177.3)	1,740.4 (1,675.8–1,805.0)
1993–94	0.42 (0.35–0.49)	2,091.0 (2,022.3–2,159.8)	1,782.4 (1,732.9–1,831.9)
1994–95	0.47 (0.41–0.54)	1,997.5 (1,940.2–2,054.8)	1,765.0 (1,714.0–1,816.0)
<b>1995–96</b>	<b>0.67 (0.58–0.75)</b>	<b>2,047.7 (2,001.4–2,094.1)</b>	<b>1,817.6 (1,783.9–1,851.3)</b>
1996–97	0.48 (0.38–0.58)	2,140.8 (2,017.0–2,264.5)	1,880.0 (1,833.2–1,926.8)
1997–98	0	na	na
1998–99	0.24 (0.15–0.37)	1,992.0 (1,747.5–2,236.5)	1,755.6 (1,644.2–1,866.9)
1999–00	0	na	na
2000–01	0.37 (0.29–0.45)	1,848.2 (1,773.1–1,923.2)	1,698.8 (1,614.5–1,783.0)
2001–02	0.35 (0.23–0.48)	1,982.9 (1,815.0–2,150.7)	1,620.8 (1,475.8–1,765.9)

two-egg clutches ("B-egg") is laid several days after the "A-egg" (Anderson 1989), and if both eggs hatch, siblicidal interactions reduce the brood to one (usually the product of the A-egg), typically within a few days of the second chick's hatching (Humphries et al. 2006). Clutch size can be used as a proxy for overall parental ability (Clifford and Anderson 2001a, Townsend and Anderson 2007b). Clutch size and hatching success also separate siblicidal birds (two-egg clutches that hatched two nestlings) from clutches that produce a single hatchling. Siblicidal nestlings experience an elevated level of androgen hormones that singletons do not, and siblicidal behavior is associated with an adult behavior variant, which implies an organizational effect (Ferree et al. 2004; Müller et al. 2008, 2011). Similar effects could influence juvenile survival. Therefore, we examined the effects of clutch and brood size on juvenile survival by creating a ranked clutch-brood effect (CBE) variable: one-egg clutches = 1, two-egg clutch with only one egg hatched = 2, and two-egg clutches with both eggs hatched = 3.

The predictors of juvenile survival examined were sex, cohort size (CS), CBE, HD, age at 1%, culmen length (CL), wing length (WL), TWS, and the quadratic of HD, age, CL, WL, and TWS. All predictors, except sex and HD (which was transformed within cohort; see above), were standardized (z-score) before entry into the model. For the quadratic effect tests, we performed an additional transformation: a number was added to make all values positive before squaring them, because without this step the square of negative numbers would have the same value as the square of their positive counterparts. The number added was constant within a variable and differed across variables.

Not all fledglings could be used in analyses, because of incomplete data (missing measurements, dates, or tissue samples). In addition, individuals that survived to adulthood but did not have a sex determined by PCR were omitted from all analyses. A small number of eggs or chicks have been adopted by nongenetic parents after being displaced from their home nests (Humphries et al. 2006); these cases were also omitted from all analyses. These omissions were random, not systematic, and the criteria for omitting them were applied objectively, so we do not expect them to have biased our analyses. The minimum number of cases per parameter estimated was 33, which exceeded the minimum number

required to assess model significance adequately (Kline 1998).

## RESULTS

*Molecular sexing and sex ratios.*—Genomic DNA isolated from feather samples (cohorts 1998–1999 through 2000–2001) did not amplify as well as DNA isolated from blood samples (cohorts 2001–2002 to 2004–2005; Table 6). DNA in feather samples is present in much lower copy number than DNA from blood or other tissue samples, and DNA from feathers may also be somewhat degraded if it originated from cells that died as the feather matured (Leeton et al. 1993, Horvath et al. 2005). In addition, our feather samples were stored in variable conditions (inadvertently frozen and thawed) before the DNA was extracted, and samples that did not amplify appeared to contain degraded DNA in electrophoresis gels (T. J. Maness pers. obs.). Of 2,622 fledglings sexed by PCR that survived to adulthood (1,546 males and 1,078 females), only nine individuals (0.34%) had a PCR sex that did not match their adult sex (Table 6). Only two of these cases occurred in cohorts with feather sampling (Table 6), so we are confident in the accuracy of sexes determined from these feather samples despite the problems with DNA degradation. The sex mismatches could be due to mislabeled sample tubes, errors in identifying the sex of the adults, or PCR error. Regardless, the possible PCR error rate is low, and individuals with mismatched sexes were omitted from all analyses.

The fledging sex ratio did not differ from an even sex ratio except in 1998–1999 and 2000–2001, when it was male biased (Fig. 2A). The overall fledging sex ratio suggested a male bias, with marginal statistical significance (sex ratio = 0.519, 95% confidence interval [CI]: 0.505–0.532;  $\chi^2 = 3.64$ ,  $df = 1$ ,  $P = 0.056$ ). Cohort size explained 74.8% of the variation in fledging sex ratio ( $r = -0.86$ ,  $P = 0.01$ ). Generally, the fledging sex ratio became less male biased as cohort size increased. Variation in the fledging sex ratio explained more variation in the return sex ratio ( $F = 626.7$ ,  $df = 2$  and  $5$ ,  $P < 0.001$ ,  $r^2 = 0.96$ ) than cohort size ( $r^2 = 0.86$ ,  $P = 0.002$ ). A cohort's return sex ratio exceeded, or tended to exceed, its fledging sex ratio in all seven cohorts, and the 95% CI excluded 0.5 in all cohorts except 1999–2000 (Fig. 2A).

How important is male-biased juvenile survival in the ontogeny of the male-biased return sex

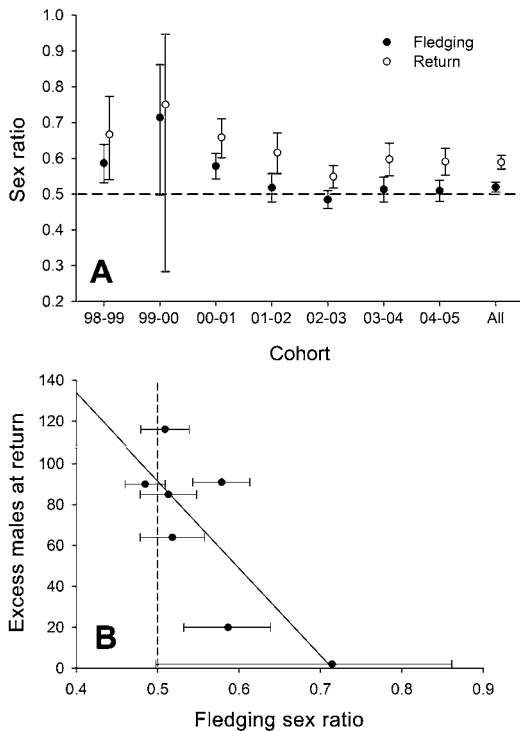


FIG. 2. (A) Fledging and return sex ratios for seven cohorts: 1998–1999, 1999–2000, 2000–2001, 2001–2002, 2002–2003, 2003–2004, and 2004–2005. Reference line indicates an even sex ratio; brackets show 95% confidence intervals. The fledging sex ratio did not differ from an even sex ratio in 1999–2000 ( $\chi^2 = 1.26$ ,  $df = 1$ ,  $P = 0.26$ ), 2001–2002 ( $\chi^2 = 0.33$ ,  $df = 1$ ,  $P = 0.57$ ), 2002–2003 ( $\chi^2 = 0.70$ ,  $df = 1$ ,  $P = 0.40$ ), 2003–2004 ( $\chi^2 = 0.22$ ,  $df = 1$ ,  $P = 0.64$ ), and 2004–2005 ( $\chi^2 = 0.14$ ,  $df = 1$ ,  $P = 0.71$ ). In both 1998–1999 and 2000–2001, it was male biased ( $\chi^2 = 4.53$ ,  $df = 1$ ,  $P = 0.033$ ;  $\chi^2 = 9.00$ ,  $df = 1$ ,  $P = 0.003$ , respectively). (B) Number of excess males returning to the colony as adults and its relationship to fledging sex ratio. Dashed line indicates an even sex ratio. Solid line is least squares regression ( $F = 9.47$ ,  $df = 1$  and  $5$ ,  $P = 0.027$ ). Brackets show 95% confidence intervals.

ratio? The fledging sex ratio of only two cohorts (1998–1999, 2000–2001) differed from unity, so the fledging sex ratio can be identified as a demonstrated contributor to the biased return sex ratio in those cohorts only. Because these two cohorts contributed few individuals to the adult population (despite the large size of the 2000–2001 cohort at the fledgling stage; see sample sizes in Table 6), the large majority (76.2%) of excess males (the number of males minus the number of females) in the returning population come from cohorts in

which the fledging sex ratio was even (Fig. 2B). Females surviving the juvenile period returned to the colony at significantly younger ages (4.45 years, 95%CI: 4.38–4.53) than did surviving male fledglings (4.91 years, 95%CI: 4.85–4.97; Welch's  $t = 82.74$ ,  $df = 1$  and  $1881.8$ ,  $P < 0.0001$ ).

*Path analysis and predictors of juvenile survival.*—Model ranking by  $AIC_c$  gave support to five top models (a confidence set that represented  $\geq 95\%$  of total model weight; Anderson 2008) that included sex, age, and either HD, TWS, or WL (Table 8). We averaged these five models before evaluation of each parameter (Burnham et al. 2011). Sex (males coded as "1" and females as "2"), age, and HD were negative predictors of juvenile survival (Fig. 3). Males were 33% more likely than females to survive the juvenile period (Fig. 3A), and an increase in fledging age by 1 day corresponded to a 3% decrease in fledging survival probability (Fig. 3B). An increase of one standard deviation in HD resulted in a 4% decrease in survival probability (Fig. 3C). Egg laying typically begins in late September and continues until February or March but varies among years, so the number of days in a change of one standard deviation in HD varies among cohorts.

Path analysis can ascertain correlations among predictors, and the ability to examine relationships among predictors and indirect effects of variables of interest motivated our use of path analysis. Below, we explore some key relationships among predictors; the full set of correlations is presented in Figures 4 and 5. Sex and age at the 1% down stage were positively correlated (Fig. 4), meaning that females tended to attain juvenal plumage (approximately speaking, "fledge") at an older age than males (females: 104.1 days, 95%CI: 103.5–104.6; males: 101.9 days, 95%CI: 101.4–102.4). Because females fledged at an average age 2.2 days later than that of males, fledging age accounted for a 6.6% drop in female juvenile survival probability compared to males. Sex and HD were not related (Fig. 4), while HD and age were positively correlated. Therefore, older fledglings were more likely to come from nests that were initiated late in the breeding season, regardless of sex.

TWS and WL were both positive predictors of juvenile survival (Fig. 3). An increase in TWS of 100 g corresponded to a 1.1% increase in survival probability. The range of TWS values was 1,650 g (–1007.7 to 642.4 g), so, all else being equal (sex, age, HD, and WL), the heaviest fledgling was ~19% more likely than the lightest fledgling to

TABLE 8. Rankings of models developed with path analysis by Akaike’s information criterion corrected for small sample size (AIC<sub>c</sub>). Abbreviations: CS = cohort size, CBE = clutch–brood effect, Sex = fledgling sex, Age = age at 1%, HD = hatching date, TWS = target weight score, CL = culmen length, and WL = wing length. “q” indicates that the quadratic ( $x + x^2$ ) of that variable was tested. Parentheses indicate indirect tests of effects. *K* = number of parameters estimated in a model;  $w_i$  = Akaike weight. “RSS” is residual sums of squares of the model. “NC” indicates that the model did not converge.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model likelihood	$w_i$	<i>K</i>	RSS	Evidence ratio
Sex + Age + HD	-1,731.82	0.00	1.000	0.400	9	569	1.00
Sex + Age + TWS	-1,730.68	1.14	0.564	0.226	10	568	1.77
Sex + Age + WL	-1,729.94	1.88	0.390	0.156	10	569	2.56
Sex + Age	-1,729.41	2.41	0.299	0.120	7	572	3.34
Sex + Age + (HD)	-1,727.40	4.42	0.110	0.044	8	572	9.11
Sex + Age + CS	-1,725.50	6.32	0.042	0.017	9	572	23.58
Sex + Age + (TWS)	-1,725.39	6.43	0.040	0.016	9	572	24.90
Sex + Age + CBE	-1,723.59	8.23	0.016	0.007	10	572	61.32
Sex + Age + TWSq	-1,723.03	8.79	0.012	0.005	16	566	81.01
Age + TWS	-1,722.38	9.44	0.009	0.004	5	578	112.00
Sex + Age + CL + WL	-1,721.86	9.96	0.007	0.003	14	569	145.62
Sex + CS + CBE + HD + Age	-1,719.77	12.05	0.002	0.001	15	569	413.10
Sex + Age + HD + TWSq	-1,718.68	13.14	0.001	0.001	21	563	712.13
Age + TWSq	-1,718.52	13.30	0.001	0.001	10	575	772.89
Age + HD	-1,718.13	13.69	0.001	0.000	5	580	938.46
Age	-1,717.41	14.41	0.001	0.000	3	582	1,348.6
Sex + HDq + Age + TWS + WL	-1,717.31	14.51	0.001	0.000	25	560	1,413.4
Sex + HD + Age + TWS + CL + WL	-1,715.98	15.84	0.000	0.000	23	563	2,752.5
Age + (WL)	-1,715.42	16.40	0.000	0.000	4	582	3,644.4
Age + (HD)	-1,715.41	16.41	0.000	0.000	4	582	3,660.6
Age + (CBE)	-1,715.40	16.42	0.000	0.000	4	582	3,679.9
Age + (TWS)	-1,715.39	16.43	0.000	0.000	4	582	3,700.2
Sex + CS + CBE + HD + Age + TWS	-1,714.48	17.34	0.000	0.000	21	565	5,834.2
(Sex) + Age + TWS	-1,714.32	17.50	0.000	0.000	9	578	6,319.9
(CBE) + HD + Age	-1,714.13	17.69	0.000	0.000	7	580	6,937.6
Age + CBE	-1,713.82	18.00	0.000	0.000	5	582	8,084.2
Age + WL	-1,713.39	18.43	0.000	0.000	5	582	10,043.6
Age + HDq	-1,712.72	19.10	0.000	0.000	11	576	14,053.6
CBE + HD + Age	-1,712.41	19.41	0.000	0.000	8	580	16,412.3
(Sex) + Age + HD	-1,712.12	19.70	0.000	0.000	8	580	18,933.9
(Sex) + Age	-1,711.37	20.45	0.000	0.000	6	582	27,568.7
Sex + Age + HDq + TWSq	-1,710.31	21.51	0.000	0.000	29	559	46,865.8
Sex + CS + CBE + HD + Age + TWS + WL	-1,707.85	23.97	0.000	0.000	27	563	1.6E+05
(Sex) + Age + (TWS)	-1,707.36	24.46	0.000	0.000	8	582	2.1E+05
Ageq	-1,707.31	24.51	0.000	0.000	8	582	2.1E+05
Sex + (CBE) + HD + Age + TWS + CL + WL	-1,705.82	26.00	0.000	0.000	28	563	4.4E+05
Sex + CS + HD + Age + TWS + CL + WL	-1,705.36	26.46	0.000	0.000	28	563	5.6E+05
Age + (TWSq)	-1,705.31	26.51	0.000	0.000	9	582	5.7E+05
HDq + Age + TWSq	-1,704.46	27.36	0.000	0.000	23	568	8.7E+05
Sex + CS + CBE + HD + Age + CL + WL	-1,703.94	27.88	0.000	0.000	26	566	1.1E+06
Sex + CBE + HD + Age + TWS + CL + WL	-1,703.73	28.09	0.000	0.000	29	563	1.3E+06
Sex + CS + CBE + Age + TWS + CL + WL	-1,697.87	33.95	0.000	0.000	29	566	2.4E+07
Sex + HDq + Age + TWS + WLq	-1,696.75	35.07	0.000	0.000	36	559	4.1E+07
Sex + CS + (CBE) + HD + Age + TWS + CL + WL	-1,695.62	36.20	0.000	0.000	33	563	7.3E+07
Sex + (CS) + CBE + HD + Age + TWS + CL + WL	-1,695.56	36.26	0.000	0.000	33	563	7.5E+07
Sex + CS + CBE + HD + Age + TWS + CL + WL	-1,693.55	38.27	0.000	0.000	34	563	2.0E+08
Sex + CS + CBE + HD + Age + TWS + (CL) + (WL)	-1,692.05	39.77	0.000	0.000	32	565	4.3E+08

(continued)

TABLE 8. Continued.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model likelihood	w <sub>i</sub>	K	RSS	Evidence ratio
CS + CBE + HD + Age + TWS + CL + WL	-1,689.99	41.83	0.000	0.000	26	573	1.2E+09
Sex + CS + CBE + HD + Age + (TWS) + CL + WL	-1,689.66	42.16	0.000	0.000	33	566	1.4E+09
Sex + CS + CBE + (HD) + Age + TWS + CL + WL	-1,689.65	42.17	0.000	0.000	33	566	1.4E+09
HDq + Age + TWSq + CL + WL	-1,687.33	44.49	0.000	0.000	34	566	4.6E+09
Sex + HDq + Age + TWSq + CL + WL	-1,685.92	45.90	0.000	0.000	42	558	9.3E+09
Sex + CS + CBE + HDq + Age + TWS + CL + WL	-1,680.77	51.05	0.000	0.000	43	560	1.2E+11
(Sex) + CS + CBE + HD + Age + TWS + CL + WL	-1,675.52	56.30	0.000	0.000	33	573	1.7E+12
Sex + CS + CBE + HD + Age + TWSq + CL + WL	-1,672.54	59.28	0.000	0.000	46	561	7.4E+12
Sex + CS + CBE + HD + Ageq + TWS + CL + WL	-1,668.70	63.12	0.000	0.000	46	563	5.1E+13
Sex + HDq + Age + TWS + CLq + WLq	-1,668.42	63.40	0.000	0.000	52	557	5.8E+13
TWS + WL	-1,666.99	64.83	0.000	0.000	5	606	1.2E+14
Sex + TWS + WL	-1,664.96	66.86	0.000	0.000	10	602	3.3E+14
Sex + TWS	-1,661.37	70.45	0.000	0.000	7	607	2.0E+15
TWS + CL + WL	-1,660.95	70.87	0.000	0.000	8	606	2.4E+15
Sex + TWS + CL + WL	-1,660.31	71.51	0.000	0.000	13	601	3.4E+15
Sex + CS + CBE + HD + TWS + CL + WL	-1,660.30	71.52	0.000	0.000	26	588	3.4E+15
Sex + TWSq	-1,660.18	71.64	0.000	0.000	13	601	3.6E+15
Sex + CS + CBE + HD + Age + TWS + CLq + WLq	-1,653.06	78.76	0.000	0.000	57	559	1.3E+17
TWSq	-1,651.58	80.24	0.000	0.000	8	611	2.6E+17
TWS	-1,647.96	83.86	0.000	0.000	3	619	1.6E+18
Sex + CS + CBE + HD + (Age) + TWS + CL + WL	-1,645.95	85.87	0.000	0.000	33	588	4.4E+18
(Age) + TWS	-1,645.94	85.88	0.000	0.000	4	619	4.5E+18
Sex + CS	-1,634.03	97.79	0.000	0.000	6	623	1.7E+21
Sex + HD	-1,631.72	100.10	0.000	0.000	6	624	5.4E+21
Sex + HDq	-1,626.55	105.27	0.000	0.000	11	622	7.2E+22
Sex + CL + WL	-1,625.78	106.04	0.000	0.000	10	623	1.1E+23
WL	-1,625.33	106.49	0.000	0.000	3	631	1.3E+23
Sex + CBE + HDq + Age + TWSq + CLq + WLq	-1,624.56	107.26	0.000	0.000	74	556	2.0E+23
Sex + WL	-1,624.14	107.68	0.000	0.000	7	627	2.4E+23
CL + WL	-1,623.19	108.63	0.000	0.000	5	630	3.9E+23
HDq + Age + TWSq + WLq	-1,618.30	113.52	0.000	0.000	39	596	4.5E+24
CS	-1,607.61	124.21	0.000	0.000	3	641	9.4E+26
HD	-1,606.71	125.11	0.000	0.000	3	641	1.5E+27
Sex	-1,603.17	128.65	0.000	0.000	5	641	8.6E+27
HDq	-1,601.36	130.46	0.000	0.000	8	639	2.1E+28
Sex + CBE	-1,600.50	131.32	0.000	0.000	7	640	3.3E+28
HDq + Age + TWSq + CLq + WLq	-1,596.64	135.18	0.000	0.000	55	590	2.3E+29
Sex + HDq + Age + TWSq + CLq + WLq	-1,588.23	143.59	0.000	0.000	65	583	1.5E+31
β	-1,580.22	151.60	0.000	0.000	2	658	8.3E+32
CBE	-1,580.18	151.64	0.000	0.000	3	657	8.5E+32
Sex + HDq + Ageq + TWS + CLq + WLq							NC
Sex + HDq + Ageq + TWS + WLq							NC
Sex + HDq + Ageq + TWSq + CLq + WLq							NC
HDq + Age + TWS + CLq + WLq							NC
CS + CBE + HDq + Ageq + TWSq + CLq + WLq							NC
Sex + CBE + HDq + Ageq + TWSq + CLq + WLq							NC
Sex + CS + CBE + HDq + Ageq + TWSq + CLq + WLq							NC
Sex + CS + CBE + HDq + Ageq + TWS + CLq + WLq							NC
Sex + CS + CBE + HDq + Ageq + TWSq + CL + WL							NC

(continued)

TABLE 8. Continued.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model likelihood	w <sub>i</sub>	K	RSS	Evidence ratio
Sex + CS + CBE + HD + Ageq + TWSq + CLq + WLq							NC
Sex + CS + CBE + HDq + Ageq + TWSq							NC

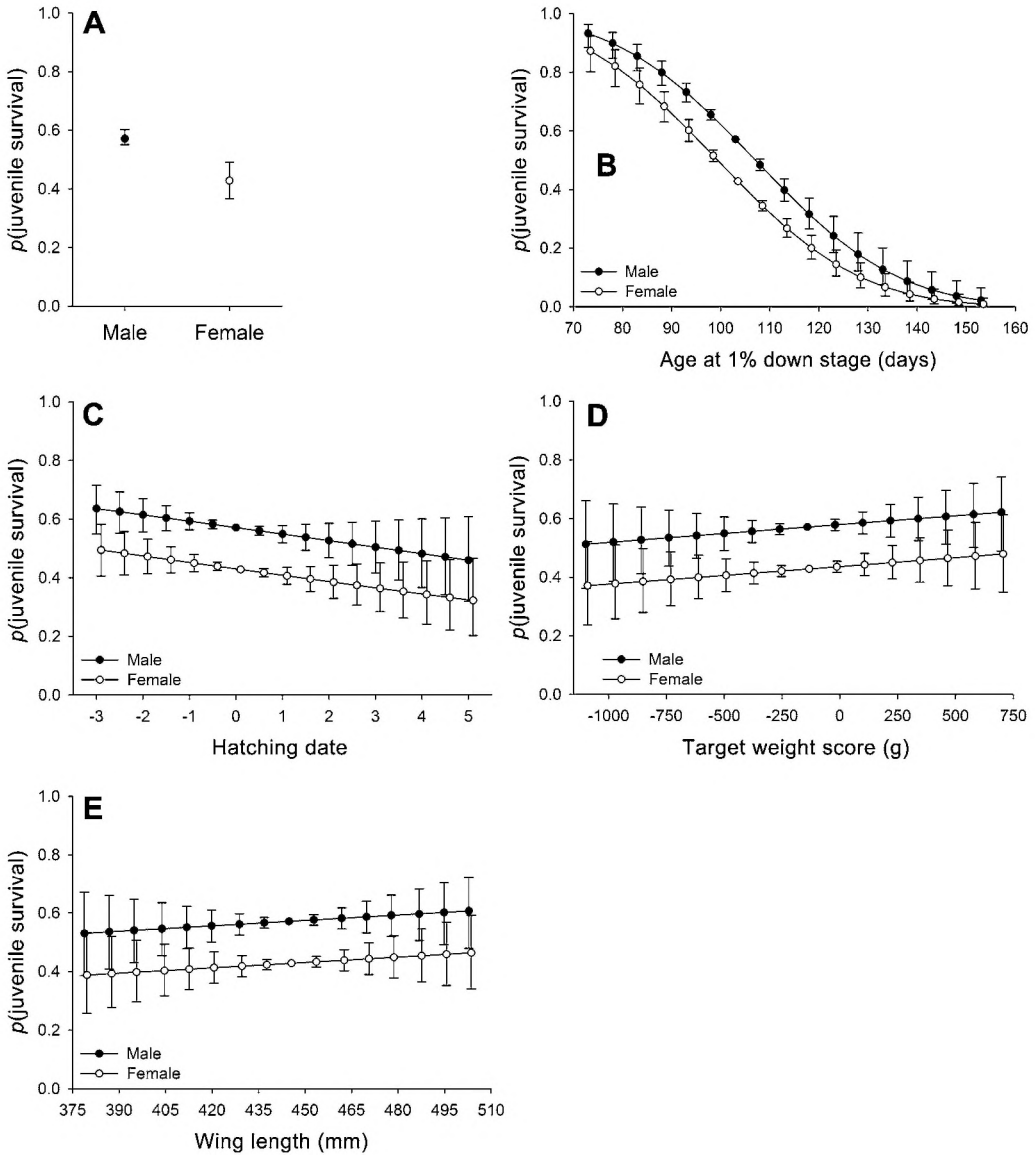


FIG. 3. Relationship between predictor variables and juvenile survival from weighted average of top path analysis models. Error bars are 95% confidence intervals calculated from the unconditional variance that included a correction for model uncertainty (see equation on p. 111 of Anderson 2008). (A) Effect of offspring sex. (B) Effect of age at which the bird reached the 1% down developmental stage. (C) Effect of hatching date, expressed as standard deviation from a given year’s z-score (see text). (D) Effect of target weight score. (E) Effect of wing length.

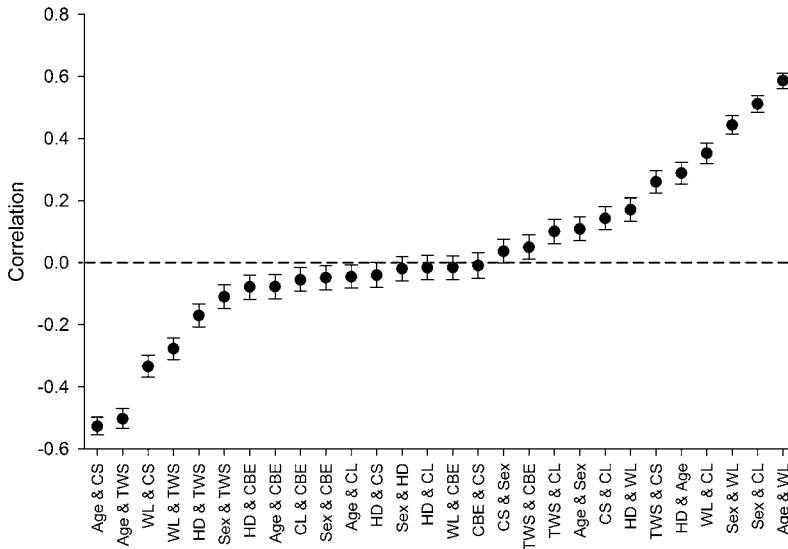


FIG. 4. Correlation between potential predictors of juvenile survival as determined by a saturated (all possible relationships included) path analysis. Brackets indicate 95% bootstrap confidence intervals. Age = age at which 1% down developmental stage was reached; CBE = clutch–brood effect; CL = culmen length; CS = cohort size; HD = hatching date; Sex = offspring sex; TWS = target weight score; and WL = wing length. For sex, males = 1 and females = 2; thus, negative parameter estimates indicate that values of males are likely to exceed those of females for that variable, and vice versa. For example, the figure indicates that male fledglings are more likely than females to have a higher weight in relation to their target weight, and that females are more likely than males to have longer culmens.

survive the juvenile period (Fig. 3D). An increase in WL of 10 mm corresponded to a 1.1% increase in survival probability. WL ranged from 377 to 497 mm, so, all else being equal, the fledgling with the longest WL was ~13% more likely to survive the juvenile period than the fledgling with the shortest WL (Fig. 3E). Female fledglings had longer wings than males (Fig. 4). This difference in WL increased female survival probability by 1.6% compared with male survival probability.

Sex and TWS were negatively correlated, while sex and WL were positively correlated (Fig. 4; an example of interpretation of correlations with discontinuous variables is given above, in the sections on study site and statistical analysis). Females were much less likely than males to reach their target weight (females: mean TWS = -165.0 g, 95%CI: -179.0 to -151.0; males: mean TWS = -112.5 g, 95%CI: -124.3 to -100.7). However, this difference in mean TWS between the sexes corresponds to only a 0.6% decrease in female survival probability compared with male survival probability. Overall, juveniles that survived to adulthood were heavier (Table 9 and Fig 3D). Within sex, heavier female and male fledglings were more likely to survive the juvenile period (Table 9 and Fig. 3D).

TWS and WL were negatively correlated, as were TWS and age, while age and WL were positively correlated; but TWS and CL were positively correlated, as were WL and CL, while age and CL were negatively correlated (Fig. 4). Thus, slowly growing nestlings were underweight and exhibited stunted growth in some structures (CL) but not others (WL). The relationship between WL and age indicates that the wing feathers have had more time to grow in older fledglings.

HD and TWS were negatively correlated, while HD and WL were positively correlated (Fig. 4). So fledglings from nests initiated late in the breeding season were underweight, and their prolonged nestling period, as indicated by age (see above), allowed more time for wing feather growth.

We examined the relationship between the predictors included in the most supported path analyses and those that were not included to explain why being female, old, underweight, small, and late-hatching makes a fledgling less likely to survive to adulthood. We also examined the correlations between predictor variables within males and females separately; although path analysis can accommodate interactions between predictors by manually creating an interaction variable, the

TABLE 9. Results of analyses of variance of individual predictor variables, with sexes combined or separate. Abbreviations: CS = cohort size, CBE = clutch-brood effect, Sex = fledgling sex, Age = age at 1% down stage (days), HD = hatching date (z-score), TWS = target weight score (g), CL = culmen length (mm), and WL = wing length (mm). Models are ranked by *P* values. Association with survival: “+” = positive, “-” = negative, and “0” = no relationship. “Critical value” is *P* corrected for multiple comparisons using the false-discovery-rate method ( $d_i$  in Benjamini and Hochberg 1995; also see Curran-Everett 2000). *P* values less than the corresponding  $d_i$  (in bold) are considered significantly different using this method.

Model	<i>F</i>	<i>P</i>	Critical value	Survivor			Nonsurvivor			Association with survival
				mean	L95	U95	mean	L95	U95	
Age	328.81	<b>5.54E-69</b>	0.006	99.69	99.26	100.12	106.32	105.74	106.90	-
TWS	164.34	<b>1.74E-36</b>	0.013	-80.64	-91.85	-69.43	-197.14	-211.00	-183.28	+
WL	109.41	<b>4.12E-25</b>	0.019	441.92	441.07	442.76	448.55	447.64	449.46	-
CS	69.20	<b>1.40E-16</b>	0.025	1,282.30	1,264.20	1,300.40	1,162.40	1,140.70	1,184.20	+
Sex	67.50	<b>3.30E-16</b>	0.031	1.41	1.38	1.44	1.57	1.54	1.59	-
HD	66.28	<b>6.05E-16</b>	0.038	-0.19	-0.23	-0.14	0.11	0.05	0.16	-
CBE	4.54	<b>0.033</b>	0.044	2.30	2.26	2.34	2.23	2.19	2.28	+
CL	3.04	0.082	0.050	102.27	102.12	102.42	102.48	102.30	102.66	0
<b>Males</b>										
Age	163.39	<b>7.44E-32</b>	0.007	99.22	98.59	99.86	105.67	104.91	106.42	-
TWS	67.33	<b>5.55E-16</b>	0.014	-71.89	-86.94	-56.84	-169.47	-187.29	-151.64	+
CS	46.07	<b>1.71E-11</b>	0.021	1,266.77	1,241.14	1,292.41	1,129.28	1,098.92	1,159.64	+
HD	44.28	<b>4.12E-11</b>	0.029	-0.17	-0.23	-0.10	0.18	0.10	0.25	-
WL	30.92	<b>3.24E-08</b>	0.036	436.22	435.25	437.20	440.50	439.35	441.66	-
CBE	5.86	<b>0.016</b>	0.043	2.35	2.29	2.40	2.24	2.18	2.31	+
CL	2.40	0.121	0.050	100.93	100.75	101.12	100.70	100.48	100.92	0
<b>Females</b>										
Age	143.6594	<b>9.03E-34</b>	0.007	100.36	99.56	101.16	106.82	106.13	107.51	-
TWS	79.6083	<b>2.23E-19</b>	0.014	-93.26	-114.08	-72.44	-218.21	-236.13	-200.28	+
CS	31.4442	<b>2.51E-08</b>	0.021	1,304.66	1,273.64	1,335.68	1,187.67	1,160.97	1,214.37	+
HD	27.4245	<b>1.91E-07</b>	0.029	-0.21	-0.29	-0.14	0.06	-0.01	0.12	-
WL	27.1345	<b>2.21E-07</b>	0.036	450.13	448.83	451.43	454.68	453.56	455.79	-
CL	6.1873	<b>0.013</b>	0.043	104.20	103.98	104.42	103.83	103.64	104.02	+
CBE	0.0029	0.957	0.050	2.23	2.16	2.29	2.23	2.17	2.28	0

effects of interactions are more easily interpreted in separate analyses (Fig. 5). The results of these separate analyses are presented below.

Female fledglings were more likely than male fledglings to be raised by low-quality parents (CBE = 1) (Figs. 4 and 6), and the fledging sex ratio of high-quality parents (CBE = 3) was male biased (Fig. 6). In addition, the fledging and return sex ratios of high-quality parents were more male biased than the fledging and return sex ratios of low-quality parents (Fig. 6). High-quality parents produced heavier fledglings with faster growth rates, and bred earlier in the season than low-quality parents (Fig. 4; correlations between CBE and TWS, age, and HD, respectively).

Nestlings in large cohorts (our proxy for environmental quality) grew faster and were heavier at

fledging than nestlings from small cohorts (Fig. 4). CS was also marginally associated with early HD and a female-biased sex ratio (Fig. 4). Structurally larger fledglings (CL) were also more likely to be produced in good years (Fig. 4). Larger fledglings (CL) were also heavier when they fledged (see above).

Within-sex examination of correlations between predictor variables showed that, during good years (indicated by large CS), males were more likely than females to fledge at younger ages and to come from nests initiated earlier in the breeding season. Female growth improved more than male growth: female CLs were longer, and females were more likely to reach their target weight as CS increased (Fig. 5). In addition, during good years, male fledglings were slightly



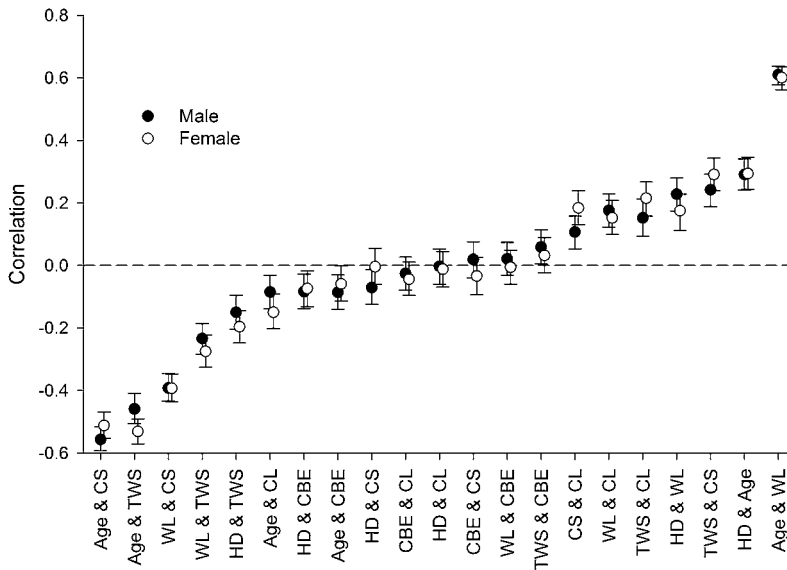


FIG. 5. Correlation between potential predictors of juvenile survival as determined by saturated (all possible relationships included) path analysis with sexes analyzed separately. Brackets indicate 95% bootstrap confidence intervals. Abbreviations of predictor names are as in Figure 4.

more likely than female fledglings to be raised by higher-quality parents (Fig. 5). Old female fledglings were much more likely than old male fledglings to be underweight and to have short CLs (Fig. 5). Fledglings from nests initiated late in the breeding season were more likely than early-hatching fledglings to have longer wings, and

this effect was slightly stronger in males than in females (Fig. 5).

*Capture-mark-recapture analysis.*—The estimated median  $\hat{c}$  for the MARK analysis was 1.99, indicating minor overdispersion in the global model (White 2002). The confidence set (Anderson 2008) comprised 13 models (Table 10), which we averaged for parameter estimation (Burnham et al. 2011). Survival probability in the averaged model varied by sex, cohort, 1% age and its quadratic (see above), TWS and its quadratic, HD and its quadratic, WL and its quadratic, CL and its quadratic, CS, and CBE. CS and CBE were negative predictors of juvenile survival, while 1% age, HD, CL, WL, and TWS were subject to stabilizing selection with regard to juvenile survival probability (see Fig. S1 in online supplemental material).

We also estimated the detection probabilities of juveniles and age of first appearance in a separate, valid (no correlated predictor variables) CMR analysis, using a larger sample of birds and with no predictor variables in MARK. This analysis included monitored as well as unmonitored (see above) fledglings. The analysis was performed in the same way as our previous analysis, except that no covariates were included, we used a single state model with resight probability at age one constrained to zero, and the total sample size was much larger: 2,676 males and 2,486 females. The

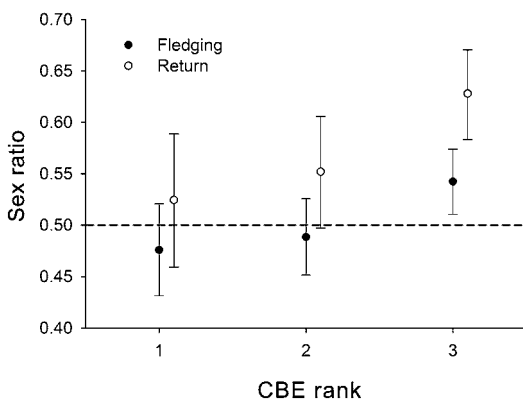


FIG. 6. Fledging and return sex ratios of the different clutch-brood effect (CBE) ranks (1 = 1-egg clutch, 2 = 2-egg clutch with only 1 egg hatching, and 3 = 2-egg clutch with both eggs hatching). Error bars are 95% bootstrap confidence intervals. Reference line indicates an even sex ratio.

TABLE 10. Ranking by QAIC<sub>c</sub> (quasi-likelihood Akaike's information criterion corrected for small sample size) of models of juvenile survival in monitored fledglings only (developed in Program MARK). Survival in the unobservable juvenile state (S:J) was held constant (.) or was allowed to vary by group (sex), by cohort (c), and by predictors of juvenile survival: CS = cohort size, CBE = clutch/brood effect, Age = age at 1%, HD = hatch date, TWS = target weight score, CL = culmen length, and WL = wing length. "q" indicates that the quadratic ( $x + x^2$ ) of that variable was tested. Survival in the adult state (S:A) varied by group (sex), resight probability in the J state was restricted to "0", resight probability of adults varied by group (sex) and age (years), transition probability between the J and A states (Psi:J-A) varied by group (sex) and age (years), and transition probability between the A and J states (Psi:J-A) was constrained to "0" in all models. Only the variables that differed between models are shown below.  $K$  = number of parameters estimated in a model;  $w_i$  = Akaike weight.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	$w_i$	Model likelihood	$K$	QDeviance
{S:J}(sex+c+Ageq+HDq+TWSq+CLq)	5,193.84	0.000	0.211	1.000	40	5,113.60
{S:J}(sex+c+Ageq+HDq+TWS+CLq)	5,194.56	0.722	0.147	0.697	39	5,116.34
{S:J}(sex+c+Ageq+HDq+TWSq+WLq+CLq)	5,194.76	0.915	0.134	0.633	42	5,110.49
{S:J}(sex+c+Ageq+HDq+TWS+WLq+CLq)	5,195.56	1.724	0.089	0.422	41	5,113.31
{S:J}(sex+c+Ageq+HDq+TWSq)	5,195.69	1.847	0.084	0.397	38	5,119.47
{S:J}(sex+c+Ageq+HDq+TWSq+WLq)	5,195.85	2.011	0.077	0.366	40	5,115.61
{S:J}(sex+c+Ageq+HDq+TWSq+CL)	5,196.80	2.958	0.048	0.228	39	5,118.57
{S:J}(sex+c+Ageq+HDq+TWSq+WL+CL)	5,197.18	3.340	0.040	0.188	40	5,116.94
{S:J}(sex+c+Age+HDq+TWSq+CLq)	5,197.49	3.649	0.034	0.161	39	5,119.26
{S:J}(sex+c+Ageq+HD+TWSq+WLq+CLq)	5,197.65	3.813	0.031	0.149	41	5,115.40
{S:J}(sex+c+Age+HDq+TWSq+WLq+CLq)	5,198.03	4.185	0.026	0.123	41	5,115.78
{S:J}(sex+c+Ageq+HDq+TWSq+WLq+CLq+CS+CBE)}	5,198.76	4.914	0.018	0.086	44	5,110.47
{S:J}(sex+c+Age+HDq+TWSq+WLq)	5,199.02	5.183	0.016	0.075	39	5,120.80
{S:J}(sex+c+Age+HDq+TWSq+WL+CL)}	5,199.79	5.947	0.011	0.051	39	5,121.56
{S:J}(sex+c+Age+HDq+TWSq+WLq+CLq+CS)}	5,200.04	6.196	0.010	0.045	42	5,115.77
{S:J}(sex+c+Age+HDq+TWS+WL+CL)}	5,201.48	7.636	0.005	0.022	38	5,125.26
{S:J}(sex+c+Ageq+TWSq+WLq+CLq)	5,201.61	7.771	0.004	0.021	40	5,121.37
{S:J}(sex+c+Age+HDq+TWSq+WLq+CLq+CS+CBE)}	5,201.75	7.908	0.004	0.019	43	5,115.47
{S:J}(sex+c+Ageq+HDq+CLq)	5,201.98	8.140	0.004	0.017	38	5,125.77
{S:J}(sex+c+Ageq+HDq+WLq+CLq)	5,202.92	9.075	0.002	0.011	40	5,122.68
{S:J}(sex+c+HD+Age+WL+TWS)}	5,203.72	9.875	0.002	0.007	36	5,131.52
{S:J}(sex+c+Age+HD+TWSq+WL+CL)}	5,204.01	10.166	0.001	0.006	38	5,127.79
{S:J}(sex+c+Ageq+TWSq)}	5,204.37	10.525	0.001	0.005	36	5,132.17
{S:J}(sex+c+HD+Age+CL+WL+TWS)}	5,205.50	11.662	0.001	0.003	37	5,131.30
{S:J}(sex+c+CBE+HD+Age+CL+WL+TWS)}	5,207.47	13.628	0.000	0.001	38	5,131.25
{S:J}(sex+c+CS+CBE+HD+Age+CL+WL+TWS)}	5,209.48	15.640	0.000	0.000	39	5,131.25
{S:J}(sex+c+Ageq)}	5,215.20	21.357	0.000	0.000	35	5,145.02
{S:J}(sex+c+Age+HD)}	5,217.93	24.087	0.000	0.000	35	5,147.75
{S:J}(sex+c+Age+WL)}	5,218.10	24.262	0.000	0.000	35	5,147.92
{S:J}(sex+c+Age)}	5,222.83	28.992	0.000	0.000	34	5,154.66
{S:J}(sex+c+HDq+TWSq+WLq+CLq)}	5,233.53	39.692	0.000	0.000	40	5,153.30
{S:J}(sex+c+Age+HDq+TWSq+WL)}	5,241.00	47.155	0.000	0.000	38	5,164.78
{S:J}(sex+c+Age+HDq+TWSq)}	5,241.98	48.141	0.000	0.000	37	5,167.78
{S:J}(sex+c+Ageq+HDq+TWSq+WL)}	5,243.01	49.166	0.000	0.000	39	5,164.78
{S:J}(sex+c+Ageq+HDq)}	5,247.71	53.865	0.000	0.000	36	5,175.51
{S:J}(sex+c+Ageq+HDq)}	5,247.71	53.865	0.000	0.000	36	5,175.51
{S:J}(sex+c+HD+Age+TWS)}	5,249.51	55.666	0.000	0.000	35	5,179.32
{S:J}(sex+c+Age+TWSq)}	5,251.52	57.676	0.000	0.000	35	5,181.33
{S:J}(sex+c+Age+TWS)}	5,255.28	61.443	0.000	0.000	35	5,185.10
{S:J}(sex+c+Age+HDq)}	5,255.48	61.636	0.000	0.000	35	5,185.29
{S:J}(sex+c+TWSq)}	5,260.78	66.940	0.000	0.000	35	5,190.60
{S:J}(sex+c+TWS+WL+CL)}	5,263.34	69.504	0.000	0.000	35	5,193.16
{S:J}(sex+c+TWS)}	5,266.31	72.468	0.000	0.000	34	5,198.14
{S:J}(sex+c+Age+HDq+TWSq+WLq+CLq+CBE)}	5,275.92	82.081	0.000	0.000	42	5,191.66

(continued)

TABLE 10. Continued.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>	Model likelihood	K	QDeviance
{S:}(sex+c+HDq)}	5,294.80	100.959	0.000	0.000	35	5,224.62
{S:}(sex+c+HD)}	5,300.58	106.744	0.000	0.000	34	5,232.41
{S:}(sex+c+CLq)}	5,312.64	118.802	0.000	0.000	35	5,242.46
{S:}(sex+c+WL)}	5,318.96	125.124	0.000	0.000	34	5,250.79
{S:}(sex+c+WLq)}	5,319.01	125.168	0.000	0.000	35	5,248.83
{S:}(sex+c+CL)}	5,320.43	126.589	0.000	0.000	34	5,252.26
{S:}(sex+c)}	5,325.76	131.916	0.000	0.000	33	5,259.59
{S:}(sex+c+CE)}	5,327.00	133.154	0.000	0.000	34	5,258.82
{S:}(sex+c+CS)}	5,329.78	135.936	0.000	0.000	35	5,259.59
{S:}(c)}	5,362.05	168.211	0.000	0.000	32	5,297.90
{S:}(sex)}	5,395.61	201.767	0.000	0.000	27	5,341.50
{S:}(.)}	5,431.92	238.080	0.000	0.000	26	5,379.82

estimated median  $\bar{c}$  for this analysis was 2.08, and the top model had much more support than the next best model did (Table 11). Survival estimates varied by sex and cohort, and recapture probabilities varied by sex and age at first appearance (Table 11 and Fig. 7). Survival probabilities of males exceeded those of females in five out of seven cohorts (Fig. 8), and recapture probabilities were high for both males and females after they were 6 years old (Fig. 7). Before age 6, females were more likely

to be recaptured than males, matching our analysis of age of first appearance above (Fig. 1).

*Logistic regression models.*—Forward and backward stepwise logistic regressions produced different top models, and nested logistic regressions yielded the same top model as the backward stepwise procedure (Table 12). The forward stepwise model included sex, 1% age, TWS and its quadratic, HD and its quadratic, and WL (Table 12). The backward stepwise model included the same

TABLE 11. Ranking by QAIC<sub>c</sub> (quasi-likelihood Akaike's information criterion corrected for small sample size) of models of juvenile survival in monitored and unmonitored fledglings (developed in Program MARK). Survival (S) was held constant (.) or was allowed to vary by group (sex), time (t = year), cohort (c), and age in years (a). Resight probability (p) was held constant (.) or was allowed to vary by group (sex), time (t = year), or age in years (a). K = number of parameters estimated in a model; w<sub>i</sub> = Akaike weight.

Model	QAIC <sub>c</sub>	ΔQAIC <sub>c</sub>	w <sub>i</sub>	Model likelihood	K	QDeviance
{S(sex*c) p(sex*a)}	10,424	0.00	1.000	1.000	50	856
{S(sex*c) p(a)}	10,476	51.62	0.000	0.000	39	929
{S(c) p(sex*a)}	10,481	56.54	0.000	0.000	36	940
{S(t) p(sex*a)}	10,560	135.74	0.000	0.000	34	1,024
{S(a) p(sex*a)}	10,622	197.49	0.000	0.000	33	1,087
{S(sex) p(sex*a)}	10,842	418.12	0.000	0.000	24	1,326
{S(.) p(sex*a)}	10,914	490.20	0.000	0.000	23	1,400
{S(.) p(a)}	10,945	520.91	0.000	0.000	12	1,453
{S(.) p(t)}	12,632	2,207.95	0.000	0.000	12	3,140
{S(sex*c) p(sex)}	16,686	6,261.74	0.000	0.000	28	7,162
{S(sex*c) p(.)}	16,691	6,267.30	0.000	0.000	27	7,169
{S(c) p(.)}	16,736	6,312.31	0.000	0.000	15	7,238
{S(a) p(.)}	16,871	6,447.26	0.000	0.000	13	7,377
{S(t) p(.)}	17,587	7,162.93	0.000	0.000	13	8,093
{S(sex) p(.)}	18,981	8,557.31	0.000	0.000	3	9,507
{S(.) p(.)}	19,058	8,634.10	0.000	0.000	2	9,586
{S(.) p(sex)}	19,059	8,634.36	0.000	0.000	3	9,584

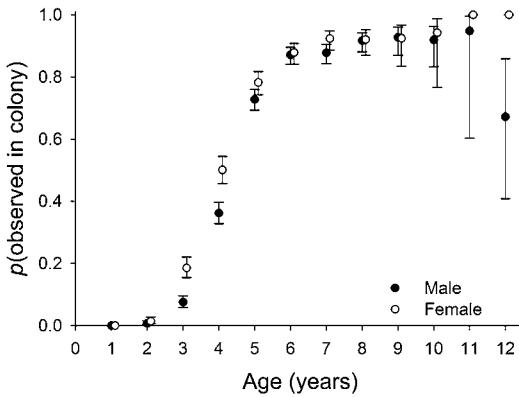


FIG. 7. Relationship between a bird's age in years and its probability of being observed in the colony as an adult at that age, as determined by a capture-mark-recapture analysis performed in Program MARK that included all unmonitored and monitored fledglings (see text). Solid circles indicate males, and open circles females. Brackets indicate 95% confidence intervals.

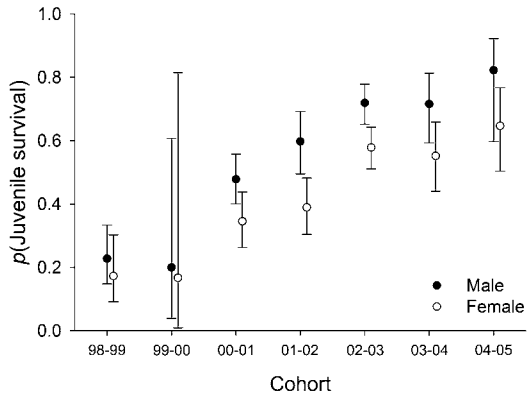


FIG. 8. Predicted male and female juvenile survival probabilities for all fledglings (monitored and unmonitored; see text) from seven cohorts (1998–1999, 1999–2000, 2000–2001, 2001–2002, 2002–2003, 2003–2004, and 2004–2005), as determined by a capture-mark-recapture analysis performed in Program MARK. Solid circles indicate males, and open circles females. Brackets indicate 95% confidence intervals.

predictors as the forward model, but also included the quadratic of WL and CL (Table 12). These same models received essentially no support in our path analysis when compared with the top path model (Table 8). The confidence set (Anderson 2008) comprised the two best-supported models, which we averaged for parameter estimation. The averaged model consisted of negative effects of sex (males were the reference group), CBE, and age at 1% down stage, a positive effect of CS, and stabilizing effects on HD, CL, WL, and TWS (see Fig. S2 in online supplemental material). Logistic regression using individual predictor variables produced one top model, which was much more supported than other models (Table 13). This model included age as a negative predictor of survival.

*Analysis of variance.*—All ANOVAs of individual predictor variables were significant except CL (Table 9). Age at 1% had the highest *F* ratio and lowest *P* value. In males, all ANOVAs except CL were significant and age at 1% had the highest *F* ratio and lowest *P* value. In females, all ANOVAs except CBE were significant and age at 1% had the highest *F* ratio and lowest *P* value. In all analyses (separate sexes and combined sexes), age, HD, and WL were negatively associated with survival, while TWS, CS, and CBE were positively associated with survival.

*Performance of statistical approaches.*—The averaged path analysis model was relatively simple (five predictors), correctly classified 66.4% of

birds, and had a likelihood *R*<sup>2</sup> (Anderson 2008) of 0.43. The averaged logistic regression model was more complex (12 variables) than the path analysis model (Tables 8, 13, and 14), correctly classified 66.3% of birds, and had an *R*<sup>2</sup> of 0.42. The CMR model was also more complex (13 variables) than the path analysis model (Tables 8, 10, and 14), correctly classified 65.2% of birds, and had an *R*<sup>2</sup> of 0.39. The unconditional standard error (Anderson 2008) of parameters estimated with path analysis was low compared with the standard errors of parameters estimated with CMR or logistic regression (Table 14). The error associated with derived parameter estimates (calculated from the equation given by each statistical approach) of male and female juvenile survival probabilities is also lowest for path analysis (Fig. 9). We draw special attention to the result that path analysis was the only statistical approach whose error estimates did not overlap with the prediction of the null model (proportion of known survivors in all analyses; Fig. 9). The performance of the ANOVAs cannot be assessed because ANOVAs are not prospective.

DISCUSSION

Ecologists have long recognized the importance of the period of early independence in birds in understanding demography, population dynamics,

TABLE 12. Ranking by Akaike's information criterion corrected for small sample size ( $AIC_c$ ) of models of juvenile survivorship performed with logistic regressions.  $\Delta AIC_c$  = change in  $AIC_c$  value between the model in question and the top model,  $K$  = number of parameters in the model, and  $w_i$  = Akaike weight; B = best model produced by backward stepwise regression, and F = best model produced by forward stepwise regression. Abbreviations: CS = cohort size, CBE = clutch-brood effect, Sex = fledgling sex, Age = age at 1% down stage (days), HD = hatching date (z-score), TWS = target weight score (g), CL = culmen length (mm), and WL = wing length (mm). "q" indicates that the quadratic ( $x + x^2$ ) of that variable was tested.

Model	$AIC_c$	$\Delta AIC_c$	Model likelihood	$w_i$	$K$	$-2\log(L)$	Evidence ratio	
Sex + HDq + Age + TWSq + WLq + [CL + CL2]	3,224	0.00	1.000	0.832	12	3,200.1	1.00	B
CS + CBE + Sex + HDq + Age + TWSq + WLq + CLq	3,227	3.46	0.177	0.147	14	3,199.3	5.64	
Sex + HDq + Age + TWS + CLq + WLq	3,233	9.10	0.011	0.009	11	3,211.0	94.68	
Sex + HDq + Age + TWSq + WL	3,234	10.07	0.007	0.005	9	3,216.0	153.61	F
Sex + HDq + Ageq + TW + CLq + WLq	3,235	11.12	0.004	0.003	12	3,211.0	259.73	
Sex + HDq + Age + TWSq + CL + WL	3,236	11.58	0.003	0.003	10	3,215.5	327.68	
Sex + Age + HDq + TWSq	3,238	13.65	0.001	0.001	8	3,221.6	922.90	
Sex + HDq + Age + TWS + WLq	3,242	17.87	0.000	0.000	9	3,223.8	7,588.60	
Sex + HDq + Age + TWS + WL	3,244	19.65	0.000	0.000	8	3,227.6	1.85E+04	
Sex + CS + CBE + HD + Age + TWS + CLq + WLq	3,249	24.72	0.000	0.000	12	3,224.6	2.33E+05	
Sex + CS + CBE + HDq + Age + TWS + CL + WL	3,249	24.80	0.000	0.000	11	3,226.7	2.43E+05	
Sex + CS + CBE + HD + Age + TWSq + CL + WL	3,253	28.50	0.000	0.000	11	3,230.4	1.54E+06	
Sex + Age + CL + WL	3,254	30.13	0.000	0.000	6	3,242.1	3.49E+06	
Sex + Age + HD + TWSq	3,256	32.14	0.000	0.000	7	3,242.1	9.54E+06	
Sex + HD + Age + TWS + CL + WL	3,258	34.02	0.000	0.000	8	3,242.0	2.45E+07	
Sex + CBE + HD + Age + TWS + CL + WL	3,260	35.97	0.000	0.000	9	3,241.9	6.46E+07	
Sex + CS + HD + Age + TWS + CL + WL	3,260	35.97	0.000	0.000	9	3,241.9	6.46E+07	
Sex + CS + CBE + HD + Age + TWS + WL	3,260	36.27	0.000	0.000	9	3,242.2	7.51E+07	
Sex + CS + CBE + HD + Age + TWS + CL + WL	3,262	37.88	0.000	0.000	10	3,241.8	1.68E+08	
Sex + Age + TWSq	3,267	43.43	0.000	0.000	6	3,255.4	2.70E+09	
HDq + Age + TWSq + CL + WL	3,268	43.67	0.000	0.000	9	3,249.6	3.04E+09	
Sex + CS + CBE + HD + Age + TWS	3,271	47.05	0.000	0.000	8	3,255.0	1.65E+10	
Sex + CS + CBE + Age + TWS + CL + WL	3,274	49.77	0.000	0.000	9	3,255.7	6.41E+10	
Sex + CS + CBE + HD + Age + CL + WL	3,275	51.27	0.000	0.000	9	3,257.2	1.36E+11	
HDq + Age + TWSq	3,276	51.94	0.000	0.000	7	3,261.9	1.90E+11	
Sex + Age + TWS	3,279	54.52	0.000	0.000	5	3,268.5	6.91E+11	
Sex + Age + WL	3,282	58.22	0.000	0.000	5	3,272.2	4.40E+12	
Sex + Age + HD	3,282	58.32	0.000	0.000	5	3,272.3	4.62E+12	
Sex + CS + CBE + HD + Age	3,286	62.14	0.000	0.000	7	3,272.1	3.12E+13	
Sex + Age	3,294	70.42	0.000	0.000	4	3,286.4	1.95E+15	
Sex + Age + CBE	3,296	71.92	0.000	0.000	5	3,285.9	4.15E+15	
Age + TWSq	3,302	78.32	0.000	0.000	5	3,292.3	1.02E+17	
CS + CBE + HD + Age + TWS + CL + WL	3,304	79.57	0.000	0.000	9	3,285.5	1.90E+17	
Age + HDq	3,312	88.22	0.000	0.000	5	3,302.2	1.44E+19	
Age + TWS	3,317	93.00	0.000	0.000	4	3,309.0	1.56E+20	
Age + HD	3,327	102.82	0.000	0.000	4	3,318.8	2.12E+22	
CBE + HD + Age	3,328	104.22	0.000	0.000	5	3,318.2	4.28E+22	
Age	3,336	112.11	0.000	0.000	3	3,330.1	2.21E+24	
Age + CBE	3,337	113.32	0.000	0.000	4	3,329.3	4.04E+24	
Age + WL	3,338	114.12	0.000	0.000	4	3,330.1	6.02E+24	
Sex + CS + CBE + HD + TWS + CL + WL	3,372	148.47	0.000	0.000	9	3,354.4	1.74E+32	
Sex + TWSq	3,418	194.12	0.000	0.000	5	3,408.1	1.42E+42	
Sex + TWS + CL + WL	3,424	200.13	0.000	0.000	6	3,412.1	2.87E+43	
Sex + TWS + WL	3,425	201.42	0.000	0.000	5	3,415.4	5.48E+43	
TWS + WL	3,442	217.52	0.000	0.000	4	3,433.5	1.71E+47	
TWS + CL + WL	3,444	219.52	0.000	0.000	5	3,433.5	4.66E+47	

(continued)

TABLE 12. Continued.

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model likelihood	w <sub>i</sub>	K	-2log(L)	Evidence ratio
Sex + TWS	3,446	221.82	0.000	0.000	4	3,437.8	1.47E+48
TWSq	3,459	234.72	0.000	0.000	4	3,450.7	9.29E+50
TWS	3,493	268.71	0.000	0.000	3	3,486.7	2.24E+58
Sex + HDq	3,507	283.02	0.000	0.000	5	3,497.0	2.87E+61
Sex + CS	3,513	289.02	0.000	0.000	4	3,505.0	5.74E+62
Sex + CL + WL	3,516	292.02	0.000	0.000	5	3,506.0	2.58E+63
Sex + HD	3,518	294.42	0.000	0.000	4	3,510.4	8.54E+63
Sex + WL	3,532	307.62	0.000	0.000	4	3,523.6	6.28E+66
CL + WL	3,543	319.22	0.000	0.000	4	3,535.2	2.07E+69
WL	3,546	321.51	0.000	0.000	3	3,539.5	6.53E+69
HDq	3,577	352.92	0.000	0.000	4	3,568.9	4.31E+76
CS	3,585	360.51	0.000	0.000	3	3,578.5	1.92E+78
Sex + CBE	3,586	361.62	0.000	0.000	4	3,577.6	3.34E+78
Sex	3,587	362.71	0.000	0.000	3	3,580.7	5.77E+78
HD	3,587	362.96	0.000	0.000	3	3,581.0	6.54E+78
CBE	3,648	424.31	0.000	0.000	3	3,642.3	1.37E+92
β	3,651	426.90	0.000	0.000	2	3,646.9	5.03E+92

and the evolution of parental care. Despite a robust effort by many investigators to identify predictors of performance during this life history stage (Table 1), we argue that no strong signal has emerged; with respect to an effect of weight, only 42 of 74 studies found a correlation (mostly positive; Table 2A). In most of these studies that detected a relationship, the possibility cannot be rejected that a stronger case can be made for a correlate of weight (hatching date and sex are examples). Our goal in the present study was to

use a new analytical approach on a large data set to avoid some of the difficulties of previous studies. Our data provide an unusually good opportunity to evaluate the dominant view that heavy weight and/or large size at independence confer high juvenile survival, and to compare the predictive ability of weight and size with those of other potential predictors. Our previous work on the pattern of juvenile survival in Nazca Boobies indicated that females survived poorly compared with males in the two cohorts examined

Table 13. Ranking by Akaike’s information criterion corrected for small sample size (AIC<sub>c</sub>) of models of juvenile survivorship performed with individual logistic regressions. ΔAIC<sub>c</sub> = change in AIC<sub>c</sub> value between the model in question and the top model, K = number of parameters in the model, and w<sub>i</sub> = Akaike weight. Abbreviations: CS = cohort size, CBE = clutch–brood effect, Sex = fledgling sex, Age = age at 1% down stage (days), HD = hatching date (z-score), TWS = target weight score (g), CL = culmen length (mm), and WL = wing length (mm).

Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Model likelihood	AIC <sub>c</sub> weight	K	-2Log(L)	Evidence ratio
Age	3,336	0.00	1.000	1.000	3	3,330.1	1.00
TWS	3,493	156.71	0.000	0.000	3	3,486.7	8.9E+33
WL	3,546	209.51	0.000	0.000	3	3,539.5	2.6E+45
CS	3,585	248.51	0.000	0.000	3	3,578.5	7.6E+53
Sex	3,587	250.71	0.000	0.000	3	3,580.7	2.3E+54
HD	3,587	250.96	0.000	0.000	3	3,581.0	2.6E+54
CBE	3,648	312.31	0.000	0.000	3	3,642.3	5.5E+67
β	3,651	314.90	0.000	0.000	2	3,646.9	2.0E+68

TABLE 14. Comparison of parameter estimates included in averaged confidence sets of models by statistical approach and the unconditional standard error (SE) associated with that estimate; SE was calculated from unconditional variance estimates that included a correction for model uncertainty (Anderson 2008). Males were the reference group for the variable sex in path analysis and logistic regression, whereas females were the reference group in the capture–mark–recapture (CMR) analysis. Abbreviations: CS = cohort size, CBE = clutch–brood effect, Sex = fledgling sex, Age = age at 1% down stage (days), HD = hatching date (z-score), TWS = target weight score (g), CL = culmen length (mm), and WL = wing length (mm). “q” indicates that the quadratic ( $x + x^2$ ) of that variable was tested.

Variable	Path analysis		Program MARK (CMR)		Logistic regression	
	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	0.535	0.057	–106.7	79.10	–5.166	0.979
Sex	–0.357	0.038	0.594	0.137	–0.600	0.109
Age	–0.443	0.045	–0.691	0.332	–0.685	0.071
Ageq			0.003	0.001		
HD	–0.056	0.035	1.446	0.841	0.720	0.240
HDq			–0.207	0.101	–0.148	0.039
TWS	0.037	0.045	0.005	0.003	1.104	0.276
TWSq			0.000	0.000	–0.120	0.036
WL	0.026	0.043	0.127	0.171	0.646	0.278
WLq			0.000	0.000	–0.061	0.033
CL			2.635	1.692	0.741	0.276
CLq			–0.013	0.008	–0.090	0.031
CBE			0.000	0.006	–0.002	0.022
CS			–0.001	0.020	0.005	0.023

(Maness et al. 2007). We argued elsewhere that the resulting male-biased adult sex ratio leads to serial monogamy (Maness and Anderson 2007), in which females represent a limiting resource for males, and females actively exchange mates for recent nonbreeders between breeding efforts (Maness and Anderson 2008). Females minimize recent costs of reproduction in their mates by this mate rotation (Maness and Anderson 2007). Another goal of this research was to determine what causes the male-biased adult sex ratio that drives this mating system.

*Sex ratios and prebreeding survival.*—For the present study, we expanded the number of cohorts providing estimates of fledging sex ratios from two (as in Maness et al. 2007) to seven. The fledging sex ratio was unbiased in the 2001–2002 and 2002–2003 cohorts, as we showed earlier (Maness et al. 2007), and also in the 1999–2000, 2003–2004, and 2004–2005 cohorts, whereas the 1998–1999 and 2000–2001 cohorts each had a male bias (Fig. 2A). Our results showed that the representation of females decreased as CS (the number of fledglings produced at our site) decreased. This suggests that fewer daughters are raised to fledging under

poor breeding conditions, possibly as a result of male-biased hatching sex ratios (our data cannot evaluate this idea), lower survival of female nestlings (see below), or both. Female nestlings can grow to a larger size than male nestlings, but they often show evidence of compromised growth (Figs. 4 and 5; Townsend et al. 2007, Apanius et al. 2008), so daughters may die more frequently during food shortages, as happens in a congener, the Blue-footed Booby (*Sula nebouxii*; Torres and Drummond 1997). This process does not imply adaptation of offspring sex ratio, although it does not exclude it. Instead, young male Nazca Boobies can tolerate a given low level of food delivery better than females, because males require less food. Females experience a developmental disadvantage more often than males, which predisposes them to mortality (especially under poor food conditions) between the end of parental care and the beginning of functional adulthood, reducing their own and their parents' fitness.

Two of the seven breeding seasons that we studied had significantly male-biased fledging sex ratios, and the overall fledging sex ratio was marginally male biased. Our results indicate that

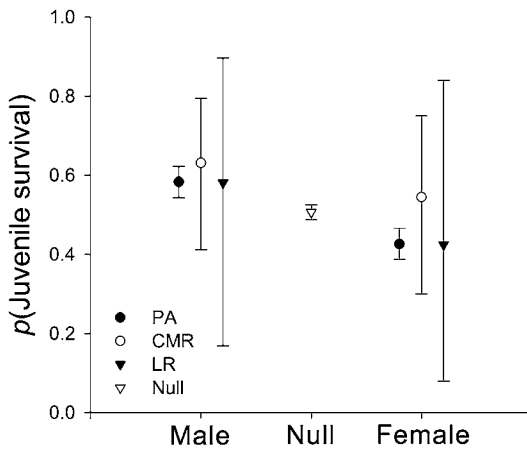


FIG. 9. Comparison of derived parameter estimates (calculated with beta estimates) of male and female juvenile survival probabilities by statistical approach (PA = path analysis, CMR = capture-mark-recapture [Program MARK], and LR = logistic regression). The null model included no predictors (see text) and was determined from the proportion of banded juveniles known to survive to adulthood (i.e., were seen in the colony as adults at least once within 6 to 12 years after fledging; see text). Error bars for model estimates are 95% confidence intervals (CIs) calculated from the unconditional variances that included a correction for model uncertainty (equation in Anderson 2008:111). Error bars for the null model are exact Bayesian 95% CIs with the assumption of no prior information (true proportion could be any number between [0,1]). While overall prediction of survival was not that different among statistical approaches, the error associated with the approaches that assume no correlation among predictors (CMR and LR) was higher than that of PA, which allows predictors to be correlated.

higher juvenile survival of males is the main driver of the consistently male-biased adult sex ratio in our study population (also see Maness et al. 2007). Male-biased fledging sex ratios, but apparently not sex-specific adult mortality (Townsend and Anderson 2007a), may have made a significant contribution to the male-biased adult sex ratio, but most of the excess males were produced by cohorts that showed high survival and no significant sex bias at fledging (Fig. 2B). Instead, excess mortality of females during the juvenile period explains most of the male bias in the adult sex ratio.

*Statistical approach.*—Compared with logistic regression and CMR analyses, path analysis produced the most parsimonious model, as well as the best performing one (in percentage of birds

correctly classified,  $R^2$ , and standard error for estimates; Table 14 and Fig. 9). The different logistic regression approaches produced different top models, which illustrates the dangers of stepwise methods. CMR can be a powerful tool in survival analyses and provide information that a path analysis cannot. For example, survival probability is a function of an individual's survival and probability of being detected. Path analysis cannot assess recapture probabilities, but this introduces no problem in the case of the Nazca Booby. We know from previous work that our recapture probabilities are high (Huyvaert and Anderson 2004, Maness and Anderson 2007, Townsend and Anderson 2007a) and that philopatry is essentially 100% (Huyvaert and Anderson 2004). Our MARK analysis that omitted covariates revealed that males and females have high recapture probabilities by age 6 years. Because juveniles in the present study had until  $\geq 6$  years of age (12 years for the oldest cohort) to demonstrate survival and had high annual detection and high annual survival probabilities, an individual's cumulative detection probability was very high (Fig. 1). Other systems with lower recapture probabilities may have less accurate results with a path analysis because survival estimation is a function of survival and detection probabilities (Burnham and Anderson 2002). In addition, CMR approaches can detect periods (e.g., year or developmental stage) of high mortality risk that path analysis cannot. For example, while it may be valuable to assess mortality risk immediately after fledging, we wanted to assess the influence of different predictors on survival from fledging to adulthood and not during an interval between these life history stages. However, CMR analyses that include correlated covariates may have difficulty with parameter estimation (Graham 2003) and cannot assess indirect effects connected to those correlations. Thus, path analysis was the best-performing statistical approach, while allowing inference based on indirect relationships among predictors. Of the predictors we examined, we found that growth rate (age at 1%), sex, HD, TWS, and WL influenced juvenile survival probabilities directly. Other predictors may influence juvenile survival indirectly through these predictors, although not strongly enough to be included in the best path analysis model.

*Growth rate.*—Age at fledging was a negative predictor of juvenile survival (Fig. 3B), and its associations with other predictor variables show that slowly growing nestlings were underweight (TWS)



and structurally (CL) smaller at fledging (Figs. 4 and 5). In addition, slowly growing nestlings were more likely to be female, to be raised by lower-quality parents (CBE), to come from nests initiated late in the breeding season (HD), and to be reared in poor-quality years (CS; Figs. 4 and 5). Most seabirds (Phaethontiformes, Procellariiformes, Sphenisciformes, Pelecaniformes, Suliformes, Alcidae, and Laridae; Ericson et al. 2006, Hackett et al. 2008, Chesser et al. 2010) rely on temporally and spatially unpredictable food resources, and parents, particularly those in long-lived species, are expected to allocate nutritional resources consistently to self-maintenance and away from reproductive effort (Erikstad et al. 1998, Apanius and Nisbet 2006, Apanius et al. 2008). Nestlings of these species are expected to bear the costs of food shortages (Mauck and Grubb 1995) and to adjust growth accordingly if possible. Slow growth is associated with high nestling mortality in Roseate Terns (*Sterna dougalli*; Nisbet et al. 1998, 1999) and Sandwich Terns (Stienen and Brenninkmeijer 2002), among other seabirds. Few studies have examined the effect of growth rate on juvenile survival (Table 1), and those that did showed mixed results. Slowly growing nestlings of Black-legged Kittiwakes were less likely to return to natal areas (Coulson and Porter 1985), whereas growth rate was not associated with juvenile survival in Common Guillemots (Harris et al. 1992) or Sandwich Terns (Stienen and Brenninkmeijer 2002). Slow growth at particular developmental stages may have important consequences for nestling survival: slow growth shortly after hatching predicted nestling mortality in Roseate Terns (Nisbet et al. 1998, 1999), whereas slow growth only during the linear growth phase predicted nestling mortality in Sandwich Terns (Stienen and Brenninkmeijer 2002).

Our results indicated that individuals that take longer to reach the 1% down developmental stage survive the juvenile period poorly but did not reveal whether slow growth at a particular nestling stage was important. However, analysis of body weight during the 2002–2003 breeding season showed that Nazca Booby offspring with shorter nestling periods (at or below median fledgling age) were 5.9% heavier across the entire nestling period than offspring with longer nestling periods (Apanius et al. 2008), which suggests that long nestling periods are associated with poor parental performance throughout the nestling period.

Our results also showed that fast growth itself was important for juvenile survival, such that the

younger of two fledglings with identical measures on all other variables would be more likely than the older fledgling to survive to adulthood. Several ideas, which are not necessarily mutually exclusive, have been put forth to explain the effect of growth rate on survival. First, maternal effects can arise from modification of egg components and composition (yolk, albumen, and overall egg mass) and can influence offspring growth, metabolism, immune function, and stress response across taxa (reviewed in Ho and Burggren 2010). For example, elevated yolk corticosterone can slow offspring growth (Hayward and Wingfield 2004, Hayward et al. 2006; but see Chin et al. 2009), whereas androgens deposited in yolk can enhance growth and muscle development of offspring (Eising et al. 2001, 2006; Groothuis and Schwabl 2002, 2008). These same compounds can affect behavior relevant to juvenile survival (Hayward and Wingfield 2004, Daisley et al. 2005, Eising et al. 2006, Uller and Olsson 2006, Tobler and Sandell 2007, Ruuskanen and Laaksonen 2010; reviewed in Biro and Stamps 2008, Smith and Blumstein 2008) and may be part of the advantage of fast growth. The external factors driving maternal effects on Nazca Booby eggs are not known but could include maternal diet during egg formation (Clifford and Anderson 2001b) and management of sibling competition (Müller et al. 2008).

Second, growth can be limited by availability of food resources provided by the parents, and also by the individual offspring's capacity to assimilate the food provided (level-2 constraints; Ricklefs et al. 1998). These constraints involve two types of tradeoff. One involves a limitation in which allocation of tissue to digestion and assimilation necessarily decreases development of other tissues and their functions (Ricklefs et al. 1998). Allocation to alimentary function when the tradeoff permits it might well lead to faster growth and could confer a survival advantage over individuals with less effective food processing while they are learning to forage as newly independent individuals. The second constraint involves allocation to growth versus other functions such as self-maintenance, activity, and thermoregulation (Ricklefs et al. 1998). Parents that are less efficient foragers may need to spend more time away from their nests to deliver the same quantity of food as more efficient foragers (e.g., Lescroël et al. 2010). Nazca Booby chicks left alone may need to divert energy from growth to thermoregulation, a constant concern at our equatorial study site, or to recovery from

often violent encounters with Non-Parental Adult Visitors (Anderson et al. 2004), which can induce stress. Chronic elevation of stress hormones has been shown to be detrimental across taxa (reviewed in Sapolsky et al. 2000), and increased stress during growth can have negative long-term effects on cognitive ability (Sapolsky et al. 2000, Kitatsky et al. 2003).

Finally, differential growth may result from variation in the quality of the nestling diet. For example, prey size, rather than total parental deliveries to broods, predicted juvenile survival in House Sparrows (Schwagmeyer and Mock 2008). Considering the diet's nutritional components, passerine nestlings are fed mostly caterpillars, yet spiders are provided during early growth, irrespective of spider availability (Naef-Daenzer et al. 2000, Magrath et al. 2004, Arnold et al. 2007b, Radford 2008). Spiders contain more of the amino acid taurine (Ramsay and Houston 2003) and, therefore, are apparently of higher nutritional quality than caterpillars (Magrath et al. 2004, Arnold et al. 2007b); in mammals, taurine is required for normal brain and visual development (Aerts and Van Assche 2002). Blue Tits supplemented with taurine as nestlings were less risk averse than controls and were better able to learn spatial tasks as juveniles (Arnold et al. 2007b). Offspring fed higher-quality food may grow faster and have a greater chance of surviving to adulthood (Schew and Rieckes 1998), but few studies have addressed the effect of growth rate on juvenile survival (Table 1). Even fewer have examined why or how growth rate may be important for survival. More work is needed in this area.

*Sex differences in juvenile survival.*—Female fledglings were less likely than male fledglings to survive the juvenile period (Fig. 3A), and this excess mortality of female juveniles is the principal cause of the consistently male-biased adult sex ratio in our study population (Fig. 2; Maness et al. 2007, Townsend and Anderson 2007a). This bias affects the mating dynamics and evolution of strategies of the population (Maness and Anderson 2007, 2008). The results presented here suggest that the bias affects recruitment decisions as well, with male juveniles returning to the colony significantly later than females (Fig. 1). Males experience more competition for mates than females do and may wait to acquire any benefits of further maturity before engaging in colony-based activities.

Female fledglings were more likely than males to be underweight, to be raised by lower-quality parents, and to be older at fledging (Figs. 4–6). HD was

another important predictor of juvenile survival (Fig. 3C) and, as CS increased, males surviving to fledging were more likely to have hatched earlier in the breeding season, whereas females were not (Fig. 5: HD and CS). These early-hatching males in large cohorts should have higher survival probabilities than females. Hence, juvenile females were more likely to die than juvenile males, because female fledglings were older than male fledglings, more underweight, produced by parents breeding later in season (in better years), and more likely to be raised by lower-quality parents (Figs. 4–6), possibly with negative maternal and genetic effects (see below on HD and CBE).

Fledging age was associated with factors that indicated slow or reduced growth, such as low TWS and short CL (Figs. 4 and 5). Older fledglings were more likely to be underweight and to have shorter culmens than younger fledglings, and this effect was more pronounced in females than in males (Fig. 5). As predicted by life history theory for long-lived organisms, Nazca Booby parents may regulate their parental effort under a cap (Apanius et al. 2008), and this effort level may not always meet the demands of their female offspring.

In addition, offspring sex had a direct effect on juvenile survival probability, independent of the other predictors in the model, which means that otherwise similar male and female offspring would have different probabilities of survival to adulthood, due to some correlate of sex that we did not measure (Fig. 3A). This might be explained in part by females being raised by lower-quality parents (see discussion of CBE below, although the indirect effect of CBE on sex and survival was not strong enough to be included among the best path models). A variety of other sex-specific factors could contribute to the direct sex effect; indeed, a recent meta-analysis of sex-specific environmental sensitivity suggests that the causation of sex differences in performance of young birds is likely multifactorial (Jones et al. 2009).

No previous study has assessed the effect of omitting this critical variable (sex) from an analysis of juvenile survival. In the case of Nazca Boobies, we repeated our path analyses with sex omitted to evaluate this effect (results not shown). In effect, this is the approach that we would have taken without data on sex, and it is the approach taken by the majority of studies in Table 1. When the effect of sex was omitted, weight and wing length were no longer significant positive predictors of survival, and culmen length became a marginally

negative predictor of survival. If we had lacked information on sex for our model, we would have made two erroneous conclusions: that weight did not influence juvenile survival, and that small structural size enhanced it. This exercise illustrates the importance of including the sex of fledglings in studies of juvenile survival.

*Body size and weight (target weight score).*—WL and TWS were positively related to juvenile survival, while CL was not (Table 8 and Fig. 3). Females (the structurally larger sex) exhibited lower, not higher, juvenile survival than males (Fig. 3). The size measures had contrasting relationships with weight: WL was negatively correlated with TWS, while the relationship between CL and TWS was positive. In addition, CL and WL were positively correlated (Figs. 4 and 5). Individual ANOVAs and logistic regression analyses indicated that birds (sexes combined and analyzed separately) that survived the juvenile period had shorter average WLs than birds that did not survive (Table 9). This could be interpreted as a size disadvantage. Yet in path analysis, multiple logistic regression, and CMR, WL was either positively associated with survival or was subject to stabilizing selection. This set of seemingly counterintuitive relationships among morphological measures illustrates the problem with using uninformed PCA or a single morphological measure to determine a BCI, particularly among individuals with growth periods of variable duration. In Nazca Boobies, culmen growth is typically complete by the 1% down stage, and WL is nearly complete, with males at 96.6% and females at 96.4% of the sex-specific adult length when offspring leave the colony (Townsend et al. 2007, Apanius et al. 2008, Maness et al. 2011). Nestlings that fledge at an older age have longer wings than individuals with growth periods of shorter duration (Figs. 4 and 5). This is almost certainly because the feathers of older fledglings have had more time to grow and not because the bone structure of the wing is longer in older individuals. Accordingly, the relationship between fledging age and CL was negative: slowly maturing fledglings were more likely to have shorter culmens (reflecting poor growth) than nestlings that reached the fledgling stage more quickly (Fig. 4). This effect was more pronounced in females (Fig. 5), which suggests that food limitation affects the growth of females more frequently.

Structurally smaller individuals are unlikely to require longer developmental periods than larger individuals of the same species, especially given that Nazca Boobies have essentially a single-chick

brood, with only ephemeral sibling competition. We showed previously, from a single cohort, that Nazca Boobies that fledged at older ages tended to be underweight for their sex throughout the nestling period (Apanius et al. 2008). For the sample of seven cohorts in the present study, nestlings that fledged at older ages had much lower TWSs than faster-growing nestlings (Figs. 4 and 5). We suggest that undernourished nestling Nazca Boobies have a developmental syndrome of slow structural growth, long maturation periods, and stunted or reduced structural growth of some features (e.g., culmen) but not others (e.g., feathers). A nestling with limited energetic resources may face developmental tradeoffs, and rather than reducing overall growth uniformly, energy could be directed toward growth of vital systems or structures, or growth could be slowed or reduced in some areas and not others (Schew and Ricklefs 1998). It may be worse for a seabird nestling approaching independence to compromise the growth of flight feathers as opposed to that of other structures, such as the culmen, because flight is required to forage when independent (Reid et al. 2000). In line with this reasoning, Grey-headed Albatross (*Diomedea chrysstoma*) chicks maintained feather and pectoral muscle growth at the expense of organ development and acquisition of fat stores during periods of reduced food availability (Reid et al. 2000). The positive relationship between WL and juvenile survival (Fig. 3), despite WL's strong association with predictors that reflect compromised growth (such as fledging age and TWS; Figs. 4 and 5), implicates satisfactory wing growth as a critical component of juvenile survival. This result demonstrates an advantage of the path model. With other variables in the model controlled, WL showed a positive relationship with survival, whereas an individual logistic regression and ANOVA found a negative association between WL and survival because the mean WL of nonsurvivors was typically longer than that of survivors (Table 9). This result partially supports the size advantage hypothesis, because a fledgling with long wings would more likely survive the juvenile period, all else being equal, but CL was not associated with survival.

TWS was a positive predictor of juvenile survival in our path analysis (Table 8 and Fig. 3), which supports the weight advantage hypothesis. Underweight fledglings were much more likely than heavier fledglings to be older at fledging and to originate from nests initiated late in the breeding season (Figs. 4 and 5). Considering seabird species,

Stienen and Brenninkmeijer (2002) suggested that the degree of dependence on parental care during the postfledging period should predict the importance of fledging weight on juvenile survival, because all studies of seabirds that have found a positive relationship between fledging weight and survival were of species that become independent before or immediately after fledging. Nazca Booby parents feed young after they fledge until just before the juveniles vacate the colony ~45.3 days later (~30% of the posthatching parental care period), and parents are highly unlikely to care for their offspring after they leave (Maness et al. 2011). Therefore, parental care extends well into the postfledging period in Nazca Boobies, and TWS was important for juvenile survival (also see Table 1), contradicting Stienen and Brenninkmeijer's (2002) proposal.

Some species of birds reach a smaller size under poor food conditions during early development, whereas in other species there is no effect on final size (Schew and Ricklefs 1998). This discrepancy may reflect variation in the importance of structural size in obtaining resources later in life. In addition to stunting structural growth, nutritional deficits in early growth can compromise learning and memory capabilities of adults (Nowicki et al. 2002, Pravosudov et al. 2005). Newly independent young seabirds must learn to locate temporally and spatially variable food sources over vast areas, often using difficult and complex foraging techniques. If young seabirds are unable to master these skills quickly because their growth was compromised, they are unlikely to survive the juvenile period. As adults, seabirds may compete for mates and nesting sites in often densely populated breeding colonies, and smaller individuals could be at a competitive disadvantage even if they survive the juvenile period.

Our results suggest that negative effects of nutritional deficits, including reduced growth and possible cognitive effects, will fall more heavily on females than on males in our study population. Few studies have examined sex-specific juvenile survival (Table 1). Our results agree with and extend the large body of work on dependent young that suggests that the larger sex in size-dimorphic species often suffers more during food shortages (reviewed in Clutton-Brock 1991), particularly in the absence of sibling competition, when larger size can be converted into a competitive advantage over smaller nestmates (Breitwisch 1989, Olsen and Cockburn 1991, Mulvihill et al. 1992, Anderson et al. 1993, Arroyo 2002, Hipkiss et al. 2002).

We found support for Lack's (1966) body-reserve advantage hypothesis and for Garnett's (1981) size advantage hypothesis. Our analytical approach allowed us to test the relative importance of these hypotheses in relation to other potential predictors of survival, and we found that both advantages can simultaneously influence juvenile survival. We emphasize here that BCIs that correct for structural size are not designed to evaluate the influence of structural size itself on survival (e.g., large and small individuals can have identical regression residual scores) and should be used with caution, if at all. Instead, an approach like path analysis allows evaluation of structural size in addition to other variables of interest in a multivariate framework. Accounting for differential growth of characters is an essential and often overlooked aspect of empirical evaluations of bird growth. Path analysis allowed us to assess effects of correlated predictors like culmen length, wing length, and TWS together in the same model, in which interactions like differential growth can be parsed. CMR and logistic regression cannot treat several correlated variables in this manner (Graham 2003) unless a principal component is calculated to combine all of these related variables into a single variable, losing information on interactive effects.

*Hatching date.*—HD predicted juvenile survival, although to a lesser degree than fledging age: male and female fledglings were less likely to survive the juvenile period if they hatched late in the breeding season (Fig. 3C). HD and fledging age were positively related (Figs. 4 and 5). Therefore, offspring fledging from nests initiated late in the breeding season were more likely to experience a protracted nestling period (Figs. 4 and 5). Fledglings from late nests exhibited the effects of poor parental care: they were underweight and took longer to reach the developmental milestone of the 1% down stage, consistent with Lack's (1954) idea that high-performing parents begin breeding at the optimum time of year and that food may become less readily available as the breeding season progresses. An equally plausible hypothesis is that food availability does not change during the breeding season and that late-breeding birds have intrinsically poor parental performance in general (rooted in age, experience, and a variety of other possible causes), making them unable to feed nestlings adequately.

Beyond its association with predictors associated with poor parental care, HD had a direct negative effect on juvenile survival (Fig. 3C). Young birds, learning to forage while still colony-based, may

face less competition and/or less depleted food resources at common foraging areas if they fledge early in the season. Juvenile Nazca Boobies vacate the colony ~45 days after reaching the 1% down stage, regardless of the date that stage is reached (Maness et al. 2011), so early-fledging birds can leave the colony early and arrive at common foraging areas before their competitors do. Juvenile Nazca Boobies apparently spend at least part of their time off the Central American coast, possibly a common area for their first year or two at least (Huyvaert and Anderson 2004). Limited data from nonbreeding adults indicate that they stay in the vicinity of the Galápagos (D. J. Anderson unpubl. data) and do not overlap with the juveniles. For birds in general, early breeding is associated with higher juvenile survival probabilities than late breeding (Table 1). Our results implicate both poor parenting and separate temporal effects, such as reduced competition for food, as drivers of the association in Nazca Boobies.

*Cohort size.*—CS, our proxy for the environmental quality during and just after the breeding season, was not directly related to juvenile survival (Table 8); rather, it influenced survival indirectly through other predictors of survival. As CS increased, TWS, a positive predictor of survival, increased, while fledging age, a negative predictor of survival, decreased (Figs. 4 and 5). Fledglings, especially females, were heavier and larger (CL) in better breeding seasons (Figs. 4 and 5), while growth rate (age at 1%), especially of males, was faster in better seasons (Figs. 4 and 5). Male fledglings hatched earlier in good breeding seasons, but the same was not true of females (Fig. 5). As CS increased, the proportion of female fledglings produced in that cohort increased marginally (Fig. 4).

Fledgling Nazca Boobies leave the colony, on average,  $45.3 \pm 10.0$  [SD] days after fledging, regardless of sex (Maness et al. 2011). This suggests that the males that fledged at younger ages and from nests initiated earlier in the breeding season did not receive more postfledging care than female fledglings but were able to leave the island earlier, perhaps arriving at common foraging grounds before their female competitors. All of these factors (younger fledging age, heavier TWS, earlier HD, and earlier colony departure dates of male fledglings in better seasons) probably contribute to the explanation of their improved survival in those seasons (Fig. 2A).

As CS increased, the proportion of female fledglings produced in that cohort increased marginally

(Fig. 4). This suggests that fewer daughters are produced in low-quality breeding seasons, that female nestlings are more likely to die in those seasons, or both.

*Clutch-brood effect.*—Our previous work has revealed correlation among various components of parental performance: pairs producing a second egg (acting primarily as insurance; Clifford and Anderson 2001b, Humphries et al. 2006) despite nutritional obstacles to its production (Clifford and Anderson 2001b) have higher success later in the breeding cycle in raising hatched chicks (Clifford and Anderson 2001a, Townsend and Anderson 2007b), and the mothers have higher survival and fecundity in future breeding seasons (Townsend and Anderson 2007b). The CBE variable served as a proxy for this positive covariance of components of parental performance in our analysis. We use the potentially ambiguous term (Wilson and Nussey 2010) “parental quality” to refer to this composite of reproductive skills, and the CBE as a proxy for parental quality.

The CBE was not directly related to juvenile survival (Table 8) but was positively related to several other predictors that suggested improved parental care, namely faster growth (age at 1%) and earlier HDs in both sexes, and increased TWS in males (Fig. 5). Parental quality is associated with the probability of juvenile survival, but indirectly, and the indirect effect is multifaceted and diffuse, manifesting itself through the CBE’s association with other predictors of juvenile survival. Like all our predictors of survival from the time of independence to joining a breeding colony, the timing of this indirect effect’s action is unknown, but it should not be assumed to be shortly after fledging, given the evidence of longer-term effects of nestling experience on later performance even into adulthood (Lindström 1999, Saino et al. 2012, Drummond and Rodríguez 2013), including longevity (Feare 2002). This result enlarges the set of fitness-related traits that show positive covariance in this species and projects the association between parental quality and reproductive outcome beyond the times of egg laying (Clifford and Anderson 2001a) and chick rearing (Clifford and Anderson 2001a, Townsend and Anderson 2007b) and into the offspring’s early adulthood.

The CBE influenced three different predictors of juvenile survival in the case of sons (HD, age, and TWS), while only influencing two in the case of daughters (HD and age; Fig. 5). Considering the past evidence in this species of a ceiling on

reproductive effort (Apanius et al. 2008) and of higher parental-care requirements for daughters than for sons (Townsend et al. 2007, Apanius et al. 2008), we interpret the stronger signal through sons as evidence that parents are more likely to reach the effort ceiling before daughters reach independence than before sons do. To caricature this interpretation in terms of TWS, high-quality parents produce many (cheap) sons at heavy TWS, and low-quality parents produce many sons with weights far below the male target weight, so an effect of parental quality is revealed by the positive correlation. But in the case of parents of daughters, neither high-quality nor low-quality parents will or can, respectively, provide enough care for a daughter to reach the female TWS, damping variation in weights of daughters and, thus, any association between parental quality and the daughter's TWS.

The fledging sex ratio became more male biased at higher values of the CBE (Fig. 6), and parents that hatched two eggs had a significantly male-biased fledging sex ratio (Fig. 6), a result that seems unlikely to reflect adaptive control of the sex ratio by parents. From the perspective of a sex allocation argument (Fisher 1930, Charnov 1982) based on a higher cost for a daughter, lower-quality parents would be expected to avoid raising daughters. Males and females have similar variances in reproductive success (Maness and Anderson 2007), so the expectation of low-quality parents raising the low-variance sex (Trivers and Willard 1973) does not apply. Daughters have longer dispersal distances than sons (Huyvaert and Anderson 2004), so both low- and high-quality parents can avoid local resource competition for nesting space (Clark 1978) by overproducing daughters. Other aspects of selection for biased offspring sex ratios (reviewed by Cockburn et al. 2002) appear not to apply to Nazca Boobies. Under this reasoning, the correlation of parental quality and offspring sex ratio must result from an unknown adaptive effect, or from a non- or maladaptive effect. Perhaps females are more negatively affected than males by the high androgen level expressed during a siblicidal event (Ferree et al. 2004, Müller et al. 2008). Siblicide occurs only in two-egg clutches, and higher-quality parents produce two-egg clutches, so parents of two-egg clutches that produced sons would be favored by selection under this scenario. Alternatively, daughters that experience siblicide could die before fledging more frequently than males do, without any manipulation of the sex ratio by high-quality parents. More work, however,

is needed before any definitive conclusions can be made.

The finding that lower-quality parents (low CBE rank) were more likely than high-quality parents to produce a daughter suggests a link between breeding conditions and the fledging sex ratio. During poor breeding conditions, low-quality parents may be less likely to breed than high-quality parents, or their offspring may be more likely to die before fledging. Also during poor breeding conditions, we suspect that daughters are more likely to die before fledging (because of their higher food requirements; Townsend et al. 2007, Apanius et al. 2008). The combination of these two effects may skew the fledging sex ratio of high-quality parents toward males, even if they produce an even sex ratio at hatching (Maness et al. 2007).

*Environmental heterogeneity.*—Different cohorts of juvenile Nazca Boobies, and different members of the same cohort, may experience different environments after becoming independent. We used cohort size as a proxy for environmental quality during the period of parental care, but it may not reflect conditions after independence reliably, for more than one reason. Chief among these is the movement of juveniles away from Galápagos: band recoveries of living and dead juveniles come from the continental coasts of the Americas from Ecuador to northern Mexico, and oceanic sites up to 3,000 km northwest of Galápagos (Huyvaert and Anderson 2004). Juveniles are thus displaced from the rearing environment in both time and space. We have not attempted to use the environmental conditions experienced by juveniles after independence to predict their survival, acknowledging significant uncertainty about the distribution of the juvenile population, which extends from the equator to outside the tropics. With better information on the location of juveniles, and on any age effect on location, informed *a priori* hypotheses can address specific potential environmental drivers of juvenile survival, such as the El Niño–Southern Oscillation.

*Conclusions.*—We draw attention to the effectiveness of the analytical approach adopted here. Our multivariate approach allowed us to disentangle the relative importance of individual predictors of juvenile survival in Nazca Boobies from a group of correlated variables and to determine which predictors influenced survival directly. We found support for both the body-reserve advantage and size advantage hypotheses, despite the difficulty in disentangling

these two possibilities. Growth rate and timing of breeding also were important for juvenile survival. Finally, bringing data from several cohorts together demonstrated that nestling growth was compromised under poor rearing conditions: overall weight fell, the number of days needed to reach fledging status increased, and the growth of some structures, but not others, was reduced. These effects were more pronounced in females and led directly or indirectly to poor survival for females between independence and breeding age. Finally, we found that lower-quality parents were more likely than high-quality parents to produce female fledglings, the larger and apparently more costly sex.

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