BREEDING OF AUSTRALIAN WHITE IBIS, STRAW-NECKED IBIS AND SILVER GULLS ON WINTER SWAMP, BALLARAT FROM 1990–1997

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Breeding populations of Silver Gull *Larus novaehollandiae*, Australian White Ibis *Threskiornis molucca* and Straw-necked Ibis *Threskiornis spinicollis* were studied, from 1990 to 1997, on Winter Swamp, Ballarat, Victoria. Silver Gulls and Australian White Ibis bred from early July to early February but there were differences amongst years. Factors affecting the variation in the starting date and length of breeding season are discussed.

Australian White Ibis had a mean clutch size of 2.25 (S.D. = 0.14) and a mode of three. There was a 6.8 times increase in the number of Australian White Ibis pulli banded each year from 1990 to 1996. Breeding effort of the population, measured by the number of ibis pulli banded per month, was influenced by the depth of water in the swamp during the previous month ($r^2 = 0.23$, $F_{1,16} = 5.00$, P = 0.040).

Silver Gull mean clutch size was 1.92 (S.D. = 0.10) and the mode, two eggs. Between 1991 and 1995 there was a 15 fold increase in the number of gull pulli banded. There was a weak relationship between the number of gull pulli banded and evaporation during the previous month ($r^2 = 0.11$, $F_{1.36} = 4.33$, P = 0.044).

INTRODUCTION

There is little doubt that Silver Gulls Larus novaehollandiae have directly benefited from additional food supplies, such as open refuse depots (Smith 1992; Smith and Carlile 1993). Increased gull abundance, particularly in urbanized areas, creates a number of problems such as fouling of domestic water supplies (Smith 1992; Smith and Carlile 1993), pathogen transmission (Monaghan *et al.* 1985) and aircraft hazards (Skira and Wapstra 1990). Undesirable population increase has required the implementation of control measures to reduce population size and breeding success. Habitat modification, culling and human disturbance appear to be successful (Skira and Wapstra 1990; Smith and Carlile 1993).

Increase in the area of agriculture under irrigation has indirectly affected the abundance of both the Australian White Ibis Threskiornis molucca and Straw-necked Ibis Threskiornis spinicollis (Carrick 1959, 1962; Marchant and Higgins 1990). Ibis have a more positive image than Silver Gulls, particularly in rural areas where Straw-necked Ibis consume plague locusts (Chortoicetes terminifera) and Australian White Ibis take freshwater crayfish (Cherax species) from irrigation channels (Carrick 1959). Overall, their range is expanding and population increasing (Blakers et al. 1984; Marchant and Higgins 1990). More recently, Australian White Ibis have been observed foraging on human food wastes in association with Silver Gulls (Marchant and Higgins 1990, pers. obs.). This has created localized problems where humans and ibis come into conflict.

Population ecology and breeding biology of Silver Gulls (Higgins and Davies 1996) and Australian White Ibis and Straw-necked Ibis (Marchant and Higgins 1990) are well known. This paper describes aspects of breeding biology of Silver Gulls, Australian White and Straw-necked Ibis on a modified wetland in western Victoria from 1990 to 1997.

STUDY AREA AND METHODS

Winter Swamp ($37^{\circ}32$ 'S, $143^{\circ}47$ 'E), a 30 ha wetland 7 km from the centre of Ballarat (Victoria), was developed for birds in 1982. Details of the structure, history and vegetation of the Swamp have been published elsewhere (Kentish 1994, Gutteridge *et al.* 1995). The catchment is 265 ha with the wetland having a maximum depth of 1.5 m, average depth of 0.75 m when full and maximum volume of 225 000 m³. Five islands were established in 1982–83 when the wetland was dry. The main breeding islands are Horseshoe, Long, North and South with a total area of approximately 0.5 ha. In 1983 various native trees and shrubs were planted on the islands. By 1997, these plants were well established on Horseshoe and Long islands. However, re-vegetation failed on North and South islands which are covered with low (less than 1.5 m), weed-dominated vegetation.

In the Ballarat region, Silver Gulls and Australian White Ibis regularly feed at the local refuse depot that was located approximately 10 km south-east of Winter Swamp. This site was closed in December 1996. A new refuse site, 13 km west of Winter Swamp, was opened in January 1997 and used by gulls and ibis. Gulls were observed opportunistically feeding on waste from local food manufacturers and at picnic areas in and around Ballarat.

Counts of Silver Gull and ibis clutches were taken at approximately weekly intervals from June to February, 1990–1997. Fieldwork was not conducted during cold (less than 5° C) or wet weather. Data were collated into 'early' (days 1–15) and 'late' (days 16–31) periods for each month. The number of surveys per period was weather dependent and it was not always possible to collect weekly data. The number of clutches and eggs recorded for each early or late monthly period was the maximum from the weekly surveys. The start of the breeding season was when eggs were found on the islands. The end of the season was when the last pulli was banded.

Breeding pairs were not individually identified, therefore it was not possible to distinguish between first, subsequent, lost or deserted clutches.

Islands were thoroughly searched and all nests located and pulli banded. To ensure that only incubating clutches were recorded, eggs found outside the nest and clutches with one or more pullus in the nest were omitted from clutch data. Obviously deserted clutches, where the eggs were heavily fouled, were not recorded.

All chicks were banded with bands supplied by the Australian Bird and Bat Banding Scheme. Silver Gull pulli were banded at approximately 2-8 days old. Ibis chicks were banded at age 8-16 days. The Department of Natural Resources and Environment (Ballarat) and the Bureau of Meteorology (Melbourne) supplied rainfall data. The nearest weather station was 1.5 km north of Winter Swamp. Evaporation data were supplied by the Bureau of Meteorology (Melbourne) for White Swam Reservoir (37°31'S, 143°55'E, elevation 507 m), approximately 15 km east of Winter Swamp. Depth was measured directly at the Swamp from 1994.

RESULTS

Australian White Ibis and Straw-necked Ibis

Australian White Ibis first bred on Winter Swamp in 1988 but this was limited to five unsuccessful clutches on Horseshoe Island. They did not breed in 1989 but returned in 1990 and continued to breed each year. The mean clutch size from 1990 to 1997 was 2.25 (S.D. = 0.14, n = 8). Clutches ranged from one to five eggs with a mode of three (41.8%) (Table 1). The maximum nest density was 836 nests/ha in late October 1996.

With the exception of 1997, incubation commenced earlier each subsequent year over the study period (Table 2). The length of the breeding season varied from four (1990; 1991) to seven months (1996), with more pulli banded in the longer seasons ($r^2 = 0.74$, $F_{1,6} = 17.5$, P = 0.006) (Table 3). The earliest start to breeding was in 1996 when Australian White Ibis commenced incubation in early July. Banding of pulli was complete from late December to early February depending on the year (Table 3). There was a 6.8 times increase in the number of pulli banded from 1990 to 1996 (Table 3).

In 1995, Straw-necked Ibis successfully bred for the first time on Winter Swamp but this was only one clutch. In 1996 there was a substantial increase in the number of Straw-necked Ibis breeding. Data for 1995 and 1996 incorporated both species because it was not possible to discriminate between Straw-necked and Australian White Ibis clutches. Differentiation between species was possible after hatching. In 1996, 550 Australian White Ibis pulli were banded compared to 32 Straw-necked Ibis (Table 3). Only Australian White Ibis bred in 1997.

 TABLE 1

 Number and size of Australian White Ibis, Straw-necked Ibis and Silver Gulls clutches found during surveys for each island (all years combined).

Australian W	hite Ibis	Threskiornis	molucca	and	Straw-necked	Ibis	Threskiornis spinicollis	
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		Clutc	h Size		
	One	Two	Three	Four	Five
North	32	46	41	7	0
South	2	6	8	1	0
Long	413	623	700	35	0
Horseshoe	1 404	1 915	2 568	124	9
Total	1 851	2 590	3 317	167	9
Silver Gull Laru	s novaehollandiae				
		Clutc	h Size		
	One	Two	Three	Four	Five
North	2 662	3 691	1 917	22	0
South	3 284	4 294	2 023	43	0
Long	4 589	7 416	4 425	9	3
Horseshoe	2 030	3 062	2 010	14	1
Total	12 565	18 463	10 375	88	4

TABLE 2

Number and kiming of Australian White Ibis and Straw-necked Ibis clutches and eggs (in parentheses) found during surveys. Australian White Ibis bred in all years shown. Skraw-necked Ibis bred in 1995 and 1996 only.

	1990	1991	1992	1993	1994	1995*	1996*	1997
Early July							12(26)	
Late July						2(3)	n.d.	
Early August						45(106)	37(82)	
Late August			11(22)	47(114)	5(6)	67(145)	127(287)	14(25)
Early September	24(52)	27 (70)	44(85)	64(159)	48(99)	84(188)	164(368)	56(107)
Late September	30(66)	n.d.	79(190)	125(290)	64(145)	156(336)	212(444)	175(376)
Early October	18(35)	42(106)	71(150)	115(278)	84(164)	175(419)	230(512)	165(405)
Late October	17(40)	31(79)	76(178)	96(228)	74(169)	141(301)	380(904)	81(171)
Early November	12(28))	8(16)	60(155)	104(224)	74(136)	138(262)	181(396)	48(96)
Late November	n.d.		43(91)	110(263)	48(100)	183(389)	33(62)	107(232)
Early December	6(12)		62(138)	36(95)	12(22)	105(252)	12(21)	73(159)
Late December			58(144)	18(35)	4(6)	16(33)	14(27)	10(14)
Early January			28(69)				2(4)	
Late January			16(39)					
Early February			8(14)					

(* = both species. n.d. = no data collected)

	1990	1991	1992	1993	1994	1995	1996	1997
Late July								
Early August								
Late August						18	3	
Early September						15	11	
Late September			19	3		23	39	6
Early October		52	28	51	66	34	27(3)	26
Late October	33	24	77	158	30	46	114(2)	90
Early November	26	25	48	19	22	76	231(10)	59
Late November	17	7	32	74	38	56(2)	59(9)	58
Early December	4	4	27	25	30	30	44(7)	36
Late December	1	1	35	79	10	80	18(1)	46
Early January			40			3	3	1
Late January			41				1	
Early February			14					
Total	81	113	361	409	196	381(2)	550(32)	322

TABLE 3 Number of Australian White¹ and Straw-necked Ibis² (in parentheses) pulli banded.

¹Total number of Australian White Ibis pulli banded = 2 413. This species was banded in all years. ²Total number of Straw-necked Ibis pulli banded = 34. This species was banded in 1995 and 1996.

In 1996, where Straw-necked Ibis nested with Australian White Ibis on Long and Horseshoe islands, nests of both species were clumped and close to the ground (<30 cm). Pulli (less than eight days old) of both species were found in one nest. At that age it was unlikely that chicks were able to move between nests.

Use of different islands as breeding sites varied between the three species (Table 4). Australian White Ibis bred mainly on the larger, well vegetated islands and used shrubs as nest sites on the smaller islands. On Horseshoe and Long islands, Blackwood Acacia melanoxylon, eucalypt trees and Melaleuca shrubs were chosen as nest sites. Nests were built at heights from ground level to over 5.0 m high. Lower nests (less than 0.5 m) were built on fallen branches or low shrubs. Early clutches were usually laid in trees and shrubs above 1.5 m. Nests built later tended to be lower.

When nest building was complete a small portion of green vegetation, a few green leaves or herbs, was placed in the nest. Egg laying commenced approximately one week later. Nests were frequently used for several seasons but often used nests were avoided because they were heavily fouled with excreta from the previous seasons and did not drain well after rain, were unstable, tilted and generally unsuitable as an egg platform. Excreta killed many of the supporting trees and the combined weight of a number of nests frequently caused the tree limb or shrub to break and fall. Nest proximity varied from less than 0.5 m, where several nests were built in one shrub or tree canopy, to a single nest greater than 10 m from other nests.

Little Pied Cormorants Phalacrocorax melanoleucos nested colonially with Australian White Ibis using old ibis nests built over water at a height of approximately 3 m.

Silver Gull

Silver Gulls bred continuously on North and South but also used Long and Horseshoe islands (Table 4). Clutches were between one and five eggs. Modal clutch size was two eggs (44.9%) (Table 1). Mean clutch size from 1990 to 1997 was 1.92 (S.D. = 0.10, n = 8) (Table 5). Maximum nest density was 2 950 nests/ha in early August 1995. There was a 15 fold increase in the number of pulli banded between 1991 and 1995 (Table 6).

The commencement of breeding activity was synchronized at the start of the breeding season, which started earlier each year from 1990 to 1996 (Table 5). The earliest breeding recorded was in July (1996). Banding was usually complete by late December but in 1995 continued to early February. The length of breeding season varied from 3.5 months (1991) to 7 months (1995). Similar to

(A–W), and S	(A-W), and Straw-necked Ibis (S-n)). Details of size and vegetation on island provided.											
Island	Horseshoe	Long	North	South								
Size	2 070 m ²	2 112 m ²	363 m²	397 m ²								
Dominant vegetation	Trees/shrubs/grass	Trees/shrubs/grass	Weeds/grass	Weeds/grass								
Year												
1990	A–W	A–W	SG	S–G								
1991	A–W	A–W	S–G	S–G								
1992	A–W	A–W	S–G	S–G								
1993	S-G/A-W	S-G/A-W	SG	S–G								
1994	S-G/A-W	S-G/A-W	S–G	S–G								
1995	S-G/S-n/A-W	S-G/A-W	S-G/A-W	SG								
1996	S-G/A-W	S-G/S-n/A-W	S-G/A-W	SG								
1997	A–W	S-G/A-W	S-G/A-W	SG/AW								

TABLE 4 Distribution of breeding colonies on islands at Winter Swamp Silver Gull (S-G), Australian White Ibis

	1990	1991	1992	1993	1994	1995	1996	1997
Early July							174(244)	
Late July					32(47)	463(743)	n.d.	
Early August					138(282)	1 458(3033)	700(1213)	
Late August			52(72)	470(931)	114(211)	1 416(2836)	964(1788)	474(745)
Early September	239(406)	2(2)	223(418)	785(1622)	616(1136)	627(1201)	472(790)	1 089(2246)
Late September	422(747)	110(187)	260(487)	743(1474)	1 348(2795)	320(679)	191(312)	684(1238)
Early October	315(618)	245(470)	218(400)	535(1041)	1 141(2378)	256(543)	175(319)	555(1131)
Late October	143(262)	202(394)	276(555)	395(817)	549(1086)	313(656)	467(601)	668(1382)
Early November	148(281)	103(189)	273(530)	294(604)	686(1451)	245(497)	386(835)	314(604)
Late November	108(207)	109(199)	177(353)	362(804)	534(1044)	193(396)	303(551)	507(954)
Early December	27(50)	71(131)	n.d.	124(273)	380(771)	236(499)	159(312)	369(709)
Late December	7(10)		70(129)	138(270)	97(171)	167(332)	119(222)	48(79)
Early January			12(23)	91(174)		30(56)	10(16)	
Late January			9(13)	69(129)				
Early Febuary				5(10)				

 TABLE 5

 Number and timing of Silver Gull clutches and eggs (in parentheses) found during surveys

(n.d. — no data collected)

ibis, more gull pulli were banded in the longer breeding seasons ($r^2 = 0.54$, $F_{1,6} = 7.10$, P = 0.037) (Table 6).

Most Silver Gulls nested on the ground. A few nests were on shrubs at heights to 1.0 m or in unoccupied Australian White Ibis nests to 2.0 m. Most nests were in open, grassed areas although some were built under shrubs and **trees**.

Rainfall, evaporation and water depth

Average rainfall for Ballarat is 711 mm per annum. Annual rainfall for the study period varied from 514 mm (1994) to 877 mm (1992). The years 1991 to 1993, and 1996 were wetter years than average (Table 7). The Swamp was dry in the summers of 1995–96 and 1997–98.

The number of gull pulli banded per month was positively affected by the previous months evaporation ($r^2 = 0.11$, $F_{1,36} = 4.33$, P = 0.044). However, there was no clear relationship between the number of gull pulli banded each month and the previous months rainfall, monthly rainfall, monthly effective rainfall (rainfall less evaporation) or water depth. The number of ibis pulli banded per month was positively influenced by the water depth during the previous month when breeding was initiated and clutches were laid ($r^2 = 0.23$, $F_{1,18} = 5.00$, P = 0.040).

	Number of Silver Gull pulli banded.												
	1990	1991	1992	1993	1994	1995	1996	1997					
Early August						15							
Late August					24	465	104						
Early September					11	830	218						
Late September	17		2	59	39	331	143	254					
Early October	78	8	13	441	906	131	24	438					
Late October	53	64	40	369	290	183	49	376					
Early November	109	45	52	183	174	120	33	160					
Late November	65	32	42	182	294	144	44	68					
Early December	18	17		24	58	51	9	40					
Late December	13		33	110	3	160	4	27					
Earl January			55	105		72							
Late January			6	28		13							
Early February						2							
Total	353	166	243	1 501	1 799	2 517	628	1 363					

TABLE 6

Total number of Silver Gull pulli banded = 8 570.

Rainfall (mm) and	l evaporation (mm) (in	parentheses)
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Year	January	February	March	April	May	June	July	August	September	October	November	December	Total
1990	4(201)	100(152)	30(115)	50(70)	11(62)	58(28)	112(31)	108(43)	52(68)	62(102)	61(136)	22(169)	670(1176)
1991	75(178)	3(166)	13(130)	37(78)	14(45)	136(33)	51(29)	105(45)	93(59)	18(116)	48(131)	138(146)	731(1156)
1992	73(131)	10(131)	30(119)	49(74)	86(43)	83(32)	47(32)	96(45)	141(51)	96(89)	84(98)	82(110)	877(955)
1993	110(146)	37(130)	29(91)	12(77)	43(52)	59(48)	97(33)	65(49)	136(71)	79(94)	55(118)	113(131)	855(1040)
1994	32(142)	84(109)	4(96)	30(78)	46(44)	82(29)	35(36)	43(52)	58(60)	48(90)	48(121)	4(194)	514(1051)
1995	51(162)	35(147)	47(111)	106(63)	65(44)	79(32)	90(28)	39(46)	39(50)	60(74)	47(102)	20(127)	678(983)
1996	40(n.d.)	79(121)	54(106)	50(53)	25(37)	85(35)	107(39)	90(40)	129(62)	56(90)	26(117)	22(150)	763(-)
1997	54(197)	12(173)	17(99)	14(66)	72(38)	35(28)	32(32)	66(44)	92(61)	47(109)	69(146)	6(171)	516(1164)

(Data supplied from Bureau of Meteorology.)

June, 1999

DISCUSSION

Methodological considerations

There are numerous logistic constraints on the viability of long-term studies that impinge on the success of a project. However, the information gained over multiple breeding seasons is essential for understanding the population ecology of long-lived species.

At Winter Swamp, the effect of weekly surveys on breeding density, number of clutches and pulli survival was not measured. However, frequent visits to colonial nesting birds affects breeding success by reducing nest density and increasing desertion and predation of eggs and chicks (Götmark 1992; Smith and Carlile 1992). Adult Silver Gulls are intolerant of displaced chicks, attacking and killing pulli found within their territory (Wheeler and Watson 1963; Higgins and Davies 1996). On Winter Swamp, this aggressive behaviour extended to other species where gulls killed ibis pulli found on the ground adjacent to gull nests.

The number of visits to the breeding population was a compromise between minimizing disruption to breeding activities and the required precision of data. A further constraint was that the regularity of surveys was hampered by unpredictable weather. Surveying at regular times, but during inclement weather, would provide useful data but may increase chick mortality. Less frequent surveys may fail to record subtle changes in the number of clutches laid and increase the difficulty of capturing and banding pulli at an appropriate age. Hand-capturing and banding young pulli was easier than attempting to capture older birds.

Counting all the clutches was technically easy. However, it was not possible to ensure that during each survey the clutch was complete as individual nests were not identified. In this study 29.6 per cent of all Silver Gull clutches were a single egg. This was within the 6 per cent to 31 per cent range found from other studies (Wheeler and Watson 1963; Wooller and Dunlop 1979, 1981; Higgins and Davies 1996). Mean clutch size at Winter Swamp was similar to studies from Western Australia (Wooller and Dunlop 1979; 1981), but smaller than other Victorian populations (Wheeler and Watson 1963). Collating the season's clutch data from Winter Swamp masked fluctuations in clutch size where birds lay larger early clutches (Wooller and Dunlop 1979, 1981; Smith and Carlile 1992).

A greater proportion of one and two egg Australian-White Ibis clutches was found in this study than elsewhere in Victoria, affecting the mean clutch size (Marchant and Higgins 1990). Some clutches at Winter Swamp may have been incomplete at the time of survey. Therefore, the mean clutch sizes may be underestimated.

Australian White Ibis and Straw-necked Ibis

The Winter Swamp ibis population, a new colony not reported by Cowling and Lowe (1981), demonstrates the ability of ibis to rapidly colonize new sites. The origin of the Winter Swamp birds was unknown but movements of ibis are extensive and nomadic (Carrick 1962; Marchant and Higgins 1990).

Ibis breeding activities increased, after initial attempts in 1988 (Kentish 1994), but not at a constant rate. It was not known what affected the variation in number of pulli although it is suspected that food, from refuse, was not a limiting factor. Each year the location of breeding colonies on the islands varied, with birds often selecting new sites. The number of seasons that a nest was used was limited. Over time bird excreta, from nestlings and parents, killed the supporting shrubs and trees. Generally there was no regrowth of the shrub or tree after ibis had ceased using it for nest support. This loss of nesting habitat may affect the long-term suitability of nest supporting trees and shrubs for ibis and other species (Baxter and Fairweather 1994; Briggs and Thornton 1995).

At Winter Swamp there was a tendency for ibis to breed earlier each year from 1990 to 1996 but no direct relationship was found between rainfall and breeding. The breeding season was similar to other studies (Marchant and Higgins 1990).

The effect of increasing water depth on initiating breeding is known (Carrick 1962). For shallow swamps deep water provides both a flooded area suitable for foraging and nest security from ground predators, such as foxes. However, water depth need not be rising at the start of the season if nests are protected, by being in trees or shrubs, from predators. Maximum water depth affected the duration of the season and longer seasons would be expected with permanent water.

Silver Gulls

Gulls favoured Winter Swamp for breeding, similar to other large artificial waterbodies with islands (Higgins and Davies 1996). Colonization and rapid population growth of gulls at Winter Swamp was attributed to the species' adaptability to novel locations and access to abundant food from local municipal refuse depot (Smith and Carlile 1992; Kentish 1994; Higgins and Davies 1996, pers. obs.).

Grassed, open areas on the islands at Winter Swamp were commonly used for breeding. Earlier studies found higher nest densities under shrubs or where nests had been covered with brush (Kentish 1994). However, such suitable sites were limited on the islands. Wheeler and Watson (1963) found that neighbouring nests are closer than usual if nesting birds are not in view of each other. The low vegetation on the islands at Winter Swamp, either due to trampling by birds or depressed grass growth under trees, may have reduced nest density.

There was considerable variation in nest densities on the islands and not all suitable habitats were used extensively by gulls. The maximum nest density, 2 932 nests/ha in August 1995, was greater than the 2 654 pairs/ha on Big Island (Wollongong) (Smith and Carlile 1992). This latter population was considered to be limited by food availability as extensive potential breeding areas were still unoccupied. Higher nest densities have been recorded, 4 402 nest/ha, for Five Islands, New South Wales (Higgins and Davies 1996).

Smith and Carlile (1992) provide evidence to suggest that the maximum number of pairs found breeding on Big Island was approximately 60 per cent of the breeding population. If this assumption was valid, for Winter Swamp, the maximum breeding population in August 1995 would approximate 2 500 pairs.

Breeding seasons, although mainly between July and December, showed considerable variation in the starting date and duration, consistent with other populations (Higgins and Davies 1996). Lack of any association of breeding with rainfall or water depth suggested seasonal breeding. In south-western Australia low rainfall during the previous year reduces food availability affecting clutch size (Wooller and Dunlop 1981).

Retention of water in the Swamp deterred ground predators allowing for an extension of the breeding seasons into late summer. The number of pulli produced per season was affected by nest density, clutch size, hatching success, length of season and food supply. In Ballarat, food availability, from refuse, was not limited.

The weak relationship between breeding and evaporation may be indicative of the importance of warmer, spring temperatures that affect breeding. In Western Australia, onset of laying strongly correlates with the timing of a spring temperature increase at the end of the previous laying period (Higgins and Davies 1996).

Commencement of breeding was synchronized but the peak period for egg laying varied amongst years. In contrast, Wooller and Dunlop (1981) found highly synchronized breeding and the peak of laying at the same time of year. Gulls at Winter Swamp were not resident and arrived each winter prior to establishing breeding territories on the islands. They left the Swamp at the end of the breeding season. Each year the time of arrival varied which affected the commencement of breeding. Other factors, such as age of the population (Ottaway *et al.* 1988), retention of pair bonds (Mills 1973) and access to food (Smith and Carlile 1992) are known to affect timing of breeding for gulls.

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