Mixed clutches at seabird colonies in west Scotland 1996–2009

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Abstract
In counts of gulls, terns, wildfowl and waders breeding on about 100 small islands along the mainland coast of west Scotland during 1996–2009, 123 clutches containing the eggs of two species ('mixed clutches') were found among 69,775 clutches of 20 species (0.18%). The annual percentage varied between 0.09% and 0.33%. Most (89%) mixed clutches contained only one egg of one of the species. The 123 mixed clutches involved 13 species, 19 species-pairs and at least 31 permutations of guest and host species. The most frequent species-pairs were Common Gull *Larus canus* and Eurasian Oystercatcher *Haematopus ostralegus*, Herring Gull *Larus argentatus* and Common Eider *Somateria mollissima*, and Common Gull and Black-headed Gull *Larus ridibundus*, these together accounting for 54% of cases. Sixteen species-pairs had been recorded in an earlier study in 1990–95, and a further six were found in 1996–2009: Common Eider and Mallard *Anas platyrhynchos* (4 mixed clutches), Herring Gull and Great Black-backed Gull *Larus marinus* (3), Common Tern *Sterna hirundo* and Arctic Tern *Sterna paradisaea* (2), Canada Goose *Branta canadensis* and Common Eider (2), Common Eider and Greylag Goose *Anser anser* (1), and Canada Goose and Greylag Goose (1). The appearance of goose eggs in mixed clutches reflected large increases in breeding numbers of both species in the area. The most frequent guest species were Eurasian Oystercatcher and Common Eider and the most frequent hosts were Common Gull and Herring Gull. Mixed clutches probably arise from attempted egg parasitism. There are records of chicks from guest eggs being reared successfully in some closely related species-pairs, but other species-pairs seem incompatible.

Introduction

Nests are sometimes found which contain the eggs of two bird species (hereafter 'mixed clutches'). They may be related to two kinds of nest parasitism. Intraspecific egg parasitism or 'egg dumping' has been recorded in at least 236 species of 43 families (Yom-Tov 2001). The more specialised interspecific brood parasitism, found in birds such as cuckoos and cowbirds, is confined to a smaller number of species and families; for example, 100 brood-parasitic species in six families were listed by Davies (2000).

Mixed clutches are more frequent than might be supposed but have received little study, probably because reports are scattered in journals with restricted distribution, such as local bird reports, and usually involve single nests encountered by chance. This paper describes mixed clutches found during systematic annual counts

of nests at seabird colonies along the mainland coast of west Scotland in 1996–2009. It follows similar work in the same area in 1990–95 (Craik 1997), but presents data for a greater number of species and a much larger number of clutches. I also identify as closely as possible the species in whose nest each mixed clutch occurred (the host species), which the earlier work made little attempt to do. Finally, I consider how mixed clutches may arise among these species and give some evidence that may be relevant.

Methods

The underlying objective of this work was to record the numbers and productivity of ground-nesting non-passerine birds breeding on small nearshore islands, in relation to presence or absence of American Mink *Neovison vison*. Data were collected from about 100 islands in sealochs, firths and sounds along the coast of the west Scottish mainland between Mallaig (57°00'N) and West Loch Tarbert (55°45'N), including islands in Loch Fyne, the Kyles of Bute and the Sound of Mull. The main bird groups were gulls (nests counted from about 10 May to early June) and terns (mid June to mid July). In practice, visits continued throughout this period because of the large number of islands, and days lost to bad weather. With few exceptions, a single visit was made to each island during this period every year.

Counts were kept of all clutches seen on each island. Most species-pairs recorded here have eggs that differ in size, shape and/or colour and are easy to detect after some experience of normal clutches (Figures 1 to 3). Such differences are distinct from, for example, the uniformly light blue eggs that sometimes occur as one, two

Figure 1. Two eggs of Common Gull *Larus canus* and one of Black-headed Gull *L. ridibundus* in Common Gull nest. Duncuan, Loch Gilp (NR8685), 25 May 2010. © *J. C. A. Craik*.

Figure 2. Two eggs of Common Gull *Larus canus* and one of Oystercatcher *Haematopus ostralegus* in Common Gull nest. Eilean Munde, Loch Leven (NN0859), 27 May 2010. © *J. C. A. Craik*.

Figure 3. Two eggs of Herring Gull *Larus argentatus* and one of Oystercatcher *Haematopus ostralegus* in Herring Gull nest. Glas Eilean, Loch Fyne (NR9185), 31 May 2010. © *J. C. A. Craik*.

or all three eggs in the clutch of a single gull or tern, or the occasional miniature, yolk-free 'runt' eggs with normal shell pigmentation that occur singly in clutches of many species. The least easy to distinguish of the species-pairs described here, in order of increasing difficulty, were: Herring Gull *Larus argentatus* and Great Black-backed Gull *L. marinus* (greater size and more brown marking of the latter); Common Gull *L. canus* and Black-headed Gull *L. ridibundus*, and Common Tern *Sterna hirundo* and Arctic Tern *S. paradisaea* (both species-pairs differ slightly in size, shape and colouring); Greylag Goose *Anser anser* and Canada Goose *Branta canadensis* (slight difference in shade and texture of the uniformly white shell).

The numbers and species of eggs in each mixed clutch were recorded and, when possible, the host species was identified. Sometimes the bird that flew from or returned to a mixed clutch was seen; otherwise the host species could often be identified from the structure of the nest. For each year, the number of mixed clutches was expressed as a percentage of the total number of clutches (mixed clutches and normal clutches with two or more eggs).

Table 1. Total numbers of clutches examined, 1996–2009. Herring Gull *Larus argentatus* includes some Lesser Black-backed Gull *L. fuscus*; nf = not found in mixed clutches. See Tables 2 & 3 for guest and host species.

Species	Clutches examined	Occurrence as one of a species-pair	Percent	Percent in 1990–1995
Common Gull *Larus canus*	10,547	55	0.52	0.39
Oystercatcher *Haematopus ostralegus*	970	47	4.85	5.88
Herring Gull *L. argentatus*	32,819	45	0.14	0.14
Common Eider *Somateria mollissima*	3,445	40	1.16	2.22
Black-headed Gull *L. ridibundus*	2,077	23	1.11	0.50
Common Tern *Sterna hirundo*	11,983	19	0.16	0.08
Great Black-backed Gull *L. marinus*	2,678	4	0.15	0.44
Mallard *Anas platyrhynchos*	61	4	6.56	nf
Canada Goose *Branta canadensis*	60	3	5.00	nf
Arctic Tern *S. paradisaea*	2,072	2	0.10	0.11
Greylag Goose *Anser anser*	88	2	2.27	nf
European Shag *Phalacrocorax aristotelis*	1,842	1	0.05	0.12
Red-breasted Merganser *Mergus serrator*	23	1	4.35	8.33
Great Cormorant *Ph. carbo*	930	nf		nf
Mute Swan *Cygnus olor*	112	nf		nf
Grey Heron *Ardea cinerea*	53	nf		nf
Common Sandpiper *Actitis hypoleucos*	7	nf		nf
Ringed Plover *Charadrius hiaticula*	7	nf		nf
Common Shelduck *Tadorna tadorna*	1	nf		nf
Total	**69,775**			

Footnote. In terms of numbers breeding in the study area, Herring and Lesser Black-backed Gulls are greatly under-represented in these data. Larger colonies of these species are normally counted as "apparently occupied territories", rather than by individual clutches (Walsh *et al.* 1995), and such colonies do not contribute to the above as clutches were not seen. Herring Gull alone outnumbered all other species above combined (pers. obs.). Greylag and Canada Geese are also very under-represented, as they begin nesting in early April and many broods of both species had left the nest by the beginning of fieldwork in mid May.

Table 2. Species-pairs involved in mixed clutches, 1996–2009. Six pairs in bold were not recorded in 1990–95. Host species: A - the number in which the host was the first-named; B - the host was the second-named; C - the host was not established.

Species-pair	Number of mixed clutches	Host species		
		A	B	C
Common Gull and Oystercatcher	28	21	2	5
Herring Gull and Common Eider	26	16	9	1
Common Gull and Black-headed Gull	12	10	2	0
Herring Gull and Oystercatcher	8	6	0	2
Herring Gull and Common Gull	7	5	1	1
Oystercatcher and Common Tern	7	5	2	0
Black-headed Gull and Common Tern	7	4	2	1
Common Gull and Common Eider	5	4	1	0
Black-headed Gull and Oystercatcher	4	2	2	0
Common Eider and Mallard	4	3	1	0
Common Gull and Common Tern	3	2	1	0
Herring Gull and Great Black-backed Gull	3	2	1	0
Common Tern and Arctic Tern	2	1	1	0
Canada Goose and Common Eider	2	2	0	0
Common Eider and Red-breasted Merganser	1	1	0	0
Great Black-backed Gull and Common Eider	1	1	0	0
Common Eider and Greylag Goose	1	1	0	0
Canada Goose and Greylag Goose	1	0	0	1
Herring Gull and European Shag	1	1	0	0
Total	**123**			

Clutches of Herring Gull are usually difficult to distinguish from those of Lesser Black-backed Gull *L. fuscus*. These two species have been combined for this analysis and the term 'Herring Gull' should be understood throughout to include a small minority of Lesser Black-backed Gulls. Clutches of Black Guillemots *Cepphus grylle* were found on many islands but have not been included in the analysis because their cavity-nesting habit makes mixed clutches unlikely, other auk species with this nesting habit do not breed in the study area, and Black Guillemot eggs have never been found in mixed clutches in this project.

Results

Between 3,659 (in 2009) and 7,135 (2000) clutches were examined annually, totalling 69,775 clutches of 20 species (Table 1). Three species, Herring Gull, Common Tern and Common Gull together accounted for 79% of the total. The number of mixed clutches found each year varied from 4 (in 2007) to 13 (2000) (mean 8.8, ± 2.6 SD, n = 14). A total of 123 mixed clutches were identified, 0.18% of the total number of clutches, the annual percentage ranging from 0.09% in 2007 to 0.33% in 2009. These values were not substantially different from those found in 1990–1995 (0.15%; 0.03–0.24%; (Craik 1997)), but the difference was not tested statistically as skill in recognising mixed clutches almost certainly increased over the years. All these values are minima, since mixed clutches probably occur, but are hard to detect, in species-pairs with similar eggs, such as Herring Gull and Lesser Black-

Table 3. Numbers of nests in which each species was host to eggs of another species. Ranges are due to uncertainty of host in 11 of the 123 mixed clutches.

Guest species - Host species	Oystercatcher	Eider	B-h Gull	C Tern	C Gull	H Gull	Mallard	G B-b Gull	Greylag	Merganser	Shag	A Tern	Canada G	Total
Common Gull	21–26	4	10	2		1–2								38–44
Herring Gull	6–8	16–17			5–6			2			1			30–34
Eider					1	9–10	3		1	1				15–16
Oystercatcher			2	5	2–7	0–2								9–16
Black-headed Gull	2			4–5	2									8–9
Common Tern	2		2–3		1							1		6–7
Canada Goose		2							0–1					2–3
Great Black-backed Gull		1				1								2
Arctic Tern				1										1
Mallard		1												1
Greylag Goose													0–1	0–1
Total	31–38	24–25	14–15	12–13	11–17	11–15	3	2	1–2	1	1	1	0–1	112–134

Most frequent guests: Oystercatcher, Eider
Most frequent hosts: Common Gull, Herring Gull

backed Gull, or Great Cormorant *Phalacrocorax carbo* and European Shag *Ph. aristotelis* (hereafter 'Shag').

Nineteen species-pairs were involved in the 123 mixed clutches (Table 2). The three most common were Common Gull and Eurasian Oystercatcher *Haematopus ostralegus* (hereafter 'Oystercatcher'), Herring Gull and Common Eider *Somateria mollissima* ('Eider'), and Common Gull and Black-headed Gull, which together accounted for 54% of all mixed clutches. Six species-pairs had not been recorded in the 1900–95 study, which recorded 16 species-pairs, of which three were not found in 1996–2009 (Common Gull and Arctic Tern; Great Black-backed Gull and Oystercatcher; Eider and Arctic Tern). Eggs of the following six species were not recorded in mixed clutches: Great Cormorant, Mute Swan *Cygnus olor*, Grey Heron *Ardea cinerea*, Common Sandpiper *Actitis hypoleucos*, Ringed Plover *Charadrius hiaticula*, Common Shelduck *Tadorna tadorna* (together 1,110 clutches, 1.6% of the total).

Table 3 shows the number of times each combination of host and guest species was found. The most frequent hosts were Common Gull and Herring Gull, which together accounted for just over half of all hosts (68–78 nests, 55–63%), no doubt because they were among the most abundant species (Table 1). The most frequent guests were Oystercatcher and Eider which together formed about half of all guests (55–63 nests, 45–51%).

Mixed clutches with six or more eggs in total (14) and those in which both species laid more than one egg (13, all but three included in the first group) are listed individually in Table 4. As in

Table 4. Details of mixed clutches containing six eggs or more in total, and those containing more than one egg of each species.

Species-pair and number of eggs	Host species
Eleven eggs	
Common Eider 6 and Mallard 5	Common Eider
Nine eggs	
Canada Goose 6 and Common Eider 3	Canada Goose
Common Eider 5 and Mallard 4	Common Eider
Red-breasted Merganser 5 and Common Eider 4	Common Eider
Eight eggs	
Mallard 7 and Common Eider 1	Mallard
Six eggs	
Common Gull 3 and Oystercatcher 3	Common Gull
Black-headed Gull 3 and Common Tern 3	Black-headed Gull
Great Black-backed Gull 3 and Common Eider 3	Great Black-backed Gull
Common Eider 4 and Herring Gull 2	Common Eider
Common Eider 5 and Herring Gull 1	Common Eider
Common Eider 5 and Herring Gull 1	Common Eider
Common Eider 5 and Herring Gull 1	Herring Gull nest, apparently incubated by Common Eider
Greylag Goose 3 and Canada Goose 3	Uncertain, both species nearby
Oystercatcher 3 and Black-headed Gull 3	Uncertain
Others with more than one egg of each species	
Common Gull 2 and Oystercatcher 2	Uncertain
Common Gull 2 and Oystercatcher 2	Common Gull
Herring Gull 2 and Common Eider 2	Herring Gull

1990–95, most mixed clutches (110, 89%) contained just one egg of one of the species, usually the guest.

Most mixed clutches contained a total number of eggs close to the normal clutch size of the host species. Thus those involving gulls, which have a normal maximum clutch of three, usually contained a total of 2–3 eggs (sometimes more). Higher totals were found in mixed clutches involving ducks and geese, which have normal clutches of 5–10 eggs depending on species. All mixed clutches with more than six eggs in total involved wildfowl as both species.

The following seven mixed clutches were all found strikingly close to a normal clutch of the guest species, and these records may help understand why mixed clutches form:

1. A Herring Gull nest with two Herring Gull eggs and one Common Gull egg was 4 m from a Common Gull nest with two (Common Gull) eggs.
2. An Eider nest with four Eider eggs and two Herring Gull eggs was 1 m from a Herring Gull nest with three eggs.

3. A Herring Gull nest with two Herring Gull eggs and one Eider egg was 4 m from an Eider nest with three eggs.
4. A Herring Gull nest with one Herring Gull egg and one Eider egg was 1.5 m from an Eider nest with five eggs (in the same Herring Gull colony as No.3).
5. A Common Gull nest with two Common Gull eggs and one Oystercatcher egg was 5 m from an Oystercatcher nest with three eggs.
6. A Common Gull nest with one Common Gull egg and one Oystercatcher egg was 2.5 m from an Oystercatcher nest with two eggs.
7. An Eider nest with three Eider eggs and one Greylag Goose egg was 2 m from a Greylag nest with six eggs.

Some records show that eggs of the guest species can hatch:
1. A Herring Gull nest contained one newly-hatched Eider chick (still wet) and two Herring Gull eggs, one of which was hatching.
2. An Oystercatcher nest contained two Oystercatcher eggs and one Black-headed Gull egg on 15 June. All the eggs were still present on 1 July, when the Black-headed Gull chick was hatching.

One observation suggested that two birds had each laid in the other's nest:
A Herring Gull nest with three Eider eggs and one Herring Gull egg was 5 m from an Eider nest (from which an Eider flew) with five Eider eggs and one Herring Gull egg.

The following record suggests involvement of three or even four birds at two nests: a Canada Goose nest with six Canada Goose eggs, some hatching, and three Eider eggs was 1 m from an Eider nest with 11 eggs (mean clutch of Eider is five, so an Eider clutch of 11 almost certainly contains the eggs of two females).

A bird may sometimes lay in the empty nest of another species, as shown by the following three of several such records of otherwise empty nests, suggesting one way in which a mixed clutch may form:
1. A Black-headed Gull nest held one Common Gull egg.
2. A Common Gull nest held two Oystercatcher eggs.
3. A Mute Swan nest held three Eider eggs, two of them partly buried in the nest material.

Discussion

The chance that a bird will become involved in a mixed clutch must be heavily influenced by local opportunity. For example, terns appear less in Table 2 than their numbers (Table 1) and breeding density might lead one to expect. This is because terns lay in June and July, after the eggs of most gulls and wildfowl have hatched. Oystercatchers are solitary nesters but lay at about the same time as gulls. An Oystercatcher breeding in a gull colony is surrounded closely by many gull nests, so the chance of a mixed clutch involving Oystercatcher is high, even though Oystercatchers are scarce relative to gulls (Table 1). Table 2 shows that the commonest mixed clutches, those of Common Gull and Oystercatcher, were mostly formed by Oystercatchers laying in Common Gull nests (21 of 23 nests with known

host species) rather than Common Gulls laying in Oystercatcher nests (2/23). The same applies to the Herring Gull and Oystercatcher pair. Similarly, in the study area Eiders tend to nest less densely than gulls (scattered singly or in small groups, rather than in large dense colonies), and more Herring Gull and Eider mixed clutches were formed by Eider laying in Herring Gull nests (16/25) than *vice versa* (9/25) (Table 2). However, most Common Gull and Black-headed Gull mixed clutches were at colonies where both species nested densely in areas closely alongside each other. The preponderance of Black-headed Gulls laying in Common Gull nests (10/12), and the low frequency *vice versa* (2/12), is less easy to understand, suggesting a difference between these two species in tendency to form mixed clutches.

The finding of mixed clutches involving Greylag and Canada Geese reflects recent population explosions of both species in the area (Craik 2002; Ogilvie 2007a, 2007b). Except for one long-established colony of Canada Geese on Eilean Balnagowan in Loch Linnhe, neither species was found breeding on any of these islands in 1990–95. A single nesting pair of Greylag Geese was first recorded in 1996 and one of Canada Geese in 1997 (Craik 2002), since when the breeding numbers and distribution of both have increased greatly. In 2009, both bred on many small islands, singly or (increasingly) in small colonies, and often closely alongside and among nests of gulls and Eiders.

Mixed clutches in other bird groups: Darwin (1873) wrote that he "could give several instances of various birds which have been known occasionally to lay their eggs in other birds' nests". He did not say which species he meant, but the context shows that the cases were interspecific. More recently, mixed clutches have been reported in many bird groups, for example Barnacle Goose *Branta leucopsis* with White-fronted Goose *Anser albifrons* (one mixed clutch), King Eider *Somateria spectabilis* (two), Red-breasted Merganser *Mergus serrator* (two) and unidentified 'seagulls' (three) (Ponomareva 1992); Scaup *Aythya* sp. with Ring-billed Gull *L. delawarensis* (Fournier 2000); Common Coot *Fulica atra* with Moorhen *Gallinula chloropus* (Forman 2003); Yellow-legged Gull *L. michahellis* with Caspian Gull *L. cachinnans* (Betleja *et al*. 2007); Long-eared owl *Asio otus* with Eurasian Magpie *Pica pica* and separately with Common Kestrel *Falco tinnunculus* (Tome 1996); Eurasian Nuthatch *Sitta europaea* with Great Tit *Parus major* (Dolenec 2002); and the three combinations of Great Tit, Blue Tit *P. caeruleus* and Pied Flycatcher *Ficedula hypoleuca* (Borgstrom 2005). The last study gives a percentage: in 40 years, three mixed clutches (one of each combination) were found in 3,691 clutches of the three species (0.08%). This percentage is similar to the annual minimum of 0.09% but lower than the total of 0.18% found in the present work, any difference probably reflecting the cavity-nesting habit of the three passerines. Craik (1997) gave references to mixed clutches involving seven other species-pairs, and further instances are cited by Cadiou & Jacob (2010). JCAC found a Common Tern nest with two eggs of Common Tern and one of Sandwich Tern on Torinturk islet in West Loch Tarbert, Argyll, west Scotland (grid reference NR810635) on 28 June 1986. The colony held 104 clutches of Common Tern. A pair of Sandwich Terns was present but no other Sandwich Tern eggs were found. Mixed clutches involving

three bird species appear not to have been recorded but must presumably occur, although in much smaller proportions than those reported here.

Outcome of mixed clutches: Timing of laying, incubation period, feeding compatibility and the degree to which the two species are related will all affect whether a guest egg is hatched and the chick is reared to independence. Some species-pairs recorded here might arguably have resulted in success, such as Common Tern and Arctic Tern, Herring Gull and Great Black-backed Gull, and Common Gull and Black-headed Gull. Some pairs seem incompatible, such as eggs of Shag in nests of Herring Gull. However, precocial chicks can walk or run within a day of hatching. The newly-hatched Eider chick in the Herring Gull nest (see Results) might well have survived by running to join an Eider brood in the care of calling adults nearby - and since Eiders nest colonially, there are usually many of these. Equally, a recently-hatched Herring Gull chick in an Eider nest would probably remain there when the Eider brood departed, shortly after hatching, and might then be adopted by a nearby Herring Gull pair - an interspecific parallel of the Herring Gull chicks that leave their parents and are adopted by other adults (Davies 2000). Such chick exchanges are not hard to imagine in dense mixed colonies like these, so it is unwise to assume that apparently unsuitable combinations must fail. Some interesting cases have been recorded. A Common Tern pair hatched an egg of a Herring Gull and raised the young to flying (Kuhlemann 1939), a pair of Roseate Terns *Sterna dougallii* hatched and raised a Sandwich Tern *S. sandvicensis* (Cadiou & Jacob 2010), and mixed broods of waterfowl are sometimes seen, e.g. Greylag Goose and Canada Goose (Soderholm 2005). In general, it is not known whether such young raised in the wild by another species then breed normally or whether their breeding attempts are impaired by faulty imprinting. One host-parasite pair in which this has been studied is Canvasback *Aythya valisineria* and Redhead *A. americana*. Davies (2000, citing personal communication from M. Sorenson) described experiments in which single young males of either species, raised in broods consisting only of the other species, later preferred females of that species. He suggested that this faulty imprinting would be mitigated in the wild, firstly by young being raised in broods containing at least a few of their own species, and secondly by the fact that in winter, when pair-formation occurs, the two species were in separate areas.

Possible reasons for mixed clutches: Proximal influences that might induce a gravid bird to lay in a nest other than her own include the sight of a nest or clutch of a conspecific, or those of another species (particularly if she herself had been reared in a nest of that species). Nest confusion would be more likely if she were young, inexperienced or slow learning. The overall density of nests and the distance between nests of two birds of a species-pair may play a part, as suggested by the unusually short distances between guest and host nests in the seven cases described above. Craik (1997) showed that mixed clutches involving species-pairs with eggs of similar size were more frequent than those with eggs of different size, which can again be seen in Table 2, and argued that intraspecific mixed clutches should be more frequent than interspecific ones, although harder to detect.

More recently, genetic fingerprinting has shown intraspecific mixed clutches to be surprisingly frequent in some groups, including gulls. High proportions of clutches may contain the eggs of more than one female, for example 34% of 160 Black-headed Gull clutches (Duda *et al*. 2008), 31% of 86 Eider clutches (Waldeck & Andersson 2006), 42% of 153 Eider clutches (Robertson *et al*. 1992), and 36% of 86 Barnacle Goose clutches (Anderholm *et al*. 2009). Egg parasitism or 'egg dumping' on this scale implies more than mere nest confusion and points to a genetic influence. It suggests that some mixed clutches found in this study, particularly those involving Black-headed Gull and Eider as guest species, were formed by birds attempting conspecific parasitism which, for some reason, laid in the nests of other species.

That reason might be nest confusion or inexperience, but seems likely to include a genetic advantage of interspecific laying. Increasing the production of young at no cost to the parent other than egg formation would be favoured and amplified by evolution. This was well argued by Davies (2000), who illustrated this with a wide range of examples of both conspecific and interspecific nest parasitism. He remarked that birds that often parasitise their own species "also occasionally parasitise other species. This could arise by mistake, but in some cases it is so frequent and appears to be so deliberate that it is likely to reflect attempts by parasites to lay more eggs by widening their net of potential hosts". Davies was referring to waterfowl, but his statement admirably describes mixed clutches in other bird groups. More work may reveal if any of the species-pairs in Table 2 include successful interspecific brood parasites (such as a newly-hatched Eider duckling running to safety from a Herring Gull nest?).

It is more difficult to explain the least compatible pairs, such as the Shag egg in a Herring Gull clutch (see Results) or the hatching Herring Gull egg in a clutch and nest of a Shag (Craik 1997), both at colonies where both species were breeding. Perhaps these are imperfections of natural selection or poor choices by laying birds - the two are synonymous. Alternatively, they may arise from a well-defined genetic imperative to lay widely and unselectively. If only one of many host species chosen by such a bird was successful and those young went on to breed, the habit of laying widely and unselectively might be propagated as a genetic by-product, explaining some of the more bizarre species-pairs. But it is questionable whether such a mechanism could persist; for example, if the offspring tended to lay in nests of the species by which they themselves had been reared, unsuccessful host species would be eliminated. The highly specialised obligate brood parasitism of birds such as Old World cuckoos probably evolved from occasional interspecific parasitism like that described here (Darwin 1873; Wyllie 1981; Davies 2000). Mixed clutches allow us a glimpse into the evolutionary history of one of the great wonders of the natural world.

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