Mussel-dropping Behaviour of Kelp Gulls

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Kelp gulls Larus dominicanus *drop black mussels* Choromytilus meridionalis *in order to break them open. This paper attempts to answer the question: What is the optimal height from which a kelp gull should drop a black mussel? The question embraces a number of interrelated problems of which some were investigated in both the field and laboratory. This involved modelling the flight dynamics of mussels and gulls.*

Swartrug-meeus Larus dominicanus *laat swartmossels* Choromytilus meridionalis *uit die lug val ten einde, hulle oop te breek. Hierdie publikasie poog om die volgende vraag te beantwoord: Wat is die optimale hoogte waarvandaan die meeu die swartmossels behoort te laat val? Die vraag behels 'n aantal verwante probleme waarvan sommige in veldwerk en in die laboratorium ondersoek is. Dit het gelei tot die modelering van die vlugdinamika van beide mossels en meeue.*

Gulls of several species in different parts of the world commonly drop hard-shelled molluscs in order to break them open.[1,2] Kelp gulls *Larus dominicanus* do this in South Africa.[3] Each gull apparently develops and refines the technique through learning by trial and error after copying other gulls. They have learnt that molluscs break more easily when dropped onto relatively hard surfaces, including rocks, roads, jetties and breakwaters, and even roofs of houses and motor cars. Along the west coast of South Africa, there are drop-sites which apparently have been used by many generations of gulls, and substantial deposits of shells of the black mussel *Choromytilus meridionalis* have accumulated there over the years.

It might at first appear that the gull's behaviour is simple. The bird flies to a point where it hovers briefly with the mussel held horizontally in its beak, drops the prey and follows it down. However, the gull must expend time and energy to search for a mussel and carry it to a drop-site. This effort is often compounded by the need to avoid marauding gulls.

This paper attempts to answer the question: what is the optimal height from which a kelp gull should drop a black mussel? The question embraces a number of interrelated problems of which some were investigated in both the field and laboratory.

Selection of black mussels and drop sites

Black mussels occur in 'colonies', both below and within the inter-tidal zone, attached to rocks in sandy areas. The mussels are washed off their rocks by waves, especially during storms in winter when wave action is severe, and are deposited on the beaches, which are patrolled by kelp gulls. Normally, the birds collect only stranded black mussels. Although kelp gulls may be seen dropping mussels at any time of the year, this behaviour is especially prevalent in winter in the south-western Cape and occurs mainly at low tide. Significant differences ($\chi^2 = 90$, d.f. 9; $\chi^2 = 133$, d.f. 10, $p < 0.005$) in the size frequency of mussels were found between collections of specimens freshly stranded along the tide line and those smashed at drop-sites in both summer and winter (Fig. 1). The collections of freshly stranded mussels contained a relative predominance of small specimens, which indicates that the gulls tend to select large mussels for dropping. In five separate field trials, adult gulls were offered a choice

Table 2. A comparison of the mussel-dropping habits of adult and juvenile kelp gulls.

No. observation days at same locality	No. adult gulls observed	No. juvenile gulls observed	No. times adults dropped mussels	No. times juveniles dropped mussels
4	87	11	212	17

Table 3. Average height (m) from which adult kelp gulls dropped black mussels (80 mm in length) onto different substrates on windless days. Figures in brackets show ranges

Sand (*A*)	Jagged rock (*B*)	Flat rock (*C*)
8.8	3.6	3.2
S.D. 0.5	S.D. 0.2	S.D. 0.2
(3.0–22.1)	(1.2–5.2)	(0.8–5.3)
$n = 30$	$n = 22$	$n = 18$

A vs C (significant at 0.01, *F*-test).

Table 1. Numbers of black mussels dropped on rock, sand or water by adult and juvenile kelp gulls along a 250-m stretch of beach with equal opportunity for dropping on the three substrates.

	Rock		Sand		Water	
	Adults	Juveniles	Adults	Juveniles	Adults	Juveniles
No. drops successful first time [a]	88	1	26	9		
No. drops unsuccessful first time [b]	47	2	76	15	20	9
No. drops unsuccessful due to pirating by other gulls	30		13	7		
Totals	165	3	115	31	20	9

[a] Mussel shell cracked and gull fed on contents. [b] Mussel shell failed to crack sufficiently for gull to feed or lost in water.

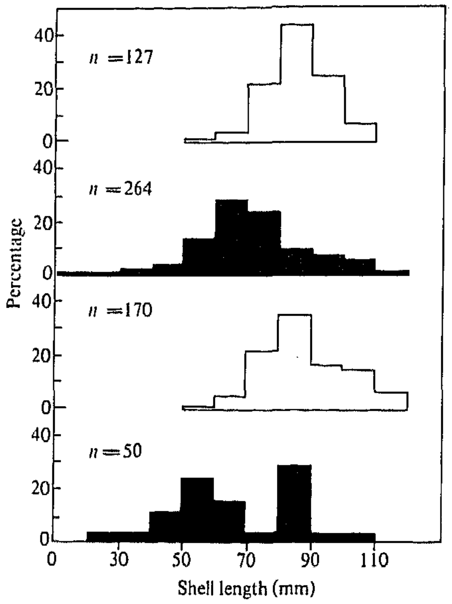


Fig. 1. Size frequency distribution of black mussels freshly stranded along the tide line (solid histograms), and broken by kelp gulls at a breakwater (open histograms) near Velddrift, south-western Cape. Upper and lower pairs of histograms are based on mussels collected in October and April respectively. The breakwater was cleared of all shells two weeks before the actual collections were made.

among mussels belonging to three size categories, namely 60–70, 80–90 and 100–110 mm. Groups of 15 mussels, comprising five specimens in each of the three size classes, were placed on the tide line. The gulls consistently ignored the small mussels and only selected the bigger specimens for dropping.

In areas of sandy beach and rock alternating in close proximity (<0.25 km apart), adult gulls flew mainly to rocky outcrops (Table 1) where they dropped their mussels. Bamboo poles had been placed at 10-m intervals along the beach, allowing the observer to estimate distance. Table 1 shows that adult birds were more successful in their mussel-dropping behaviour than juveniles (distinguished by their mottled brown and grey, immature plumage). From the data in Table 2, and assuming that the probability of observing mussel-dropping by each age group of gulls is equal, juveniles should have been observed dropping mussels 26 times in this case. In practice they dropped mussels only 17 times, which is significantly lower

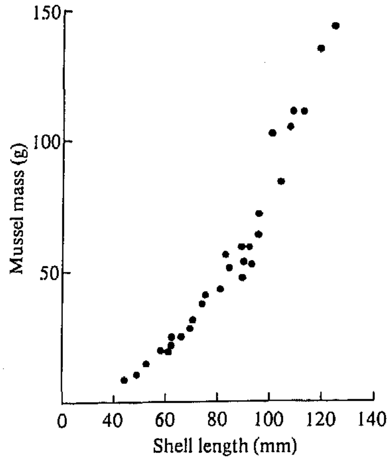


Fig. 2. Relationship between shell length and fresh whole-body mass of black mussels collected at Blaauwberg, south-western Cape.

($p < 0.05$) than would have been expected if the juveniles had been as active as adults (one-sided alternative comparison to bimodal distribution[4]).

Gulls flew more than 0.5 km, apparently to favourite, flat drop-sites, ignoring *en route* other seemingly less suitable rocky outcrops. It was presumably uneconomical for gulls to fly greater distances, since in most cases (94%, $n = 33$) in which gulls were observed feeding on mussels along long stretches of sandy beach more than 0.5 km from rocky outcrops, the birds dropped their prey onto the sand, especially that with a relatively hard, compacted surface at the water's edge.

Height from which black mussels must be dropped

Do black mussels of different sizes need to be dropped from different heights onto hard rock for their shells to be fractured? The velocity of the mussel on impact, and therefore its dynamic energy, is related to the distance through which it falls. Since the height from which a gull actually dropped a mussel was recorded indirectly by noting the time of descent, the flight dynamics of mussels could be calculated as follows. The velocity (v) of an object falling under gravity through a viscous medium is given by

$$v = \sqrt{V^2[1 - \exp(-2sg/V^2)]}$$

where V is the terminal velocity, g is the acceleration due to gravity, and s is the distance fallen. The terminal velocity is a

Fig. 3. Relationship between shell length and shell thickness of black mussels. The graph is a logarithmic fit where $y = a + b\ln x$ ($a = -0.47$, $b = 0.28$). The thickness of each of 120 shells was measured three times in the centre of the anterior adductor scar region.

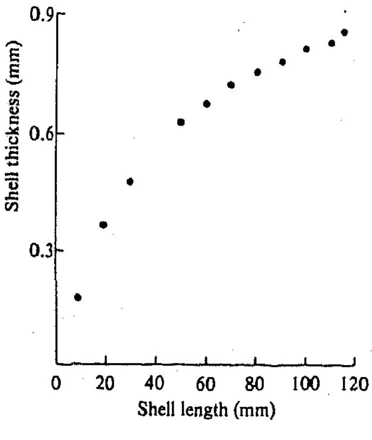


Fig. 4. Relationship between shell length and shell area (one valve only) of black mussels.

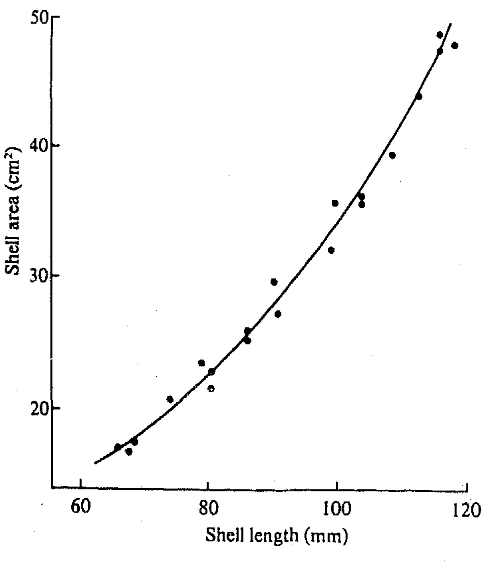
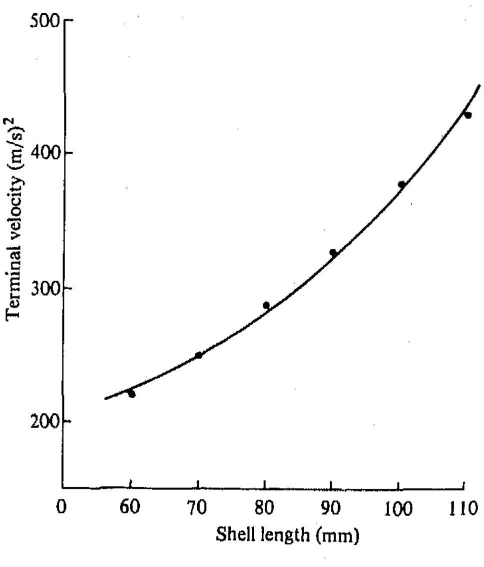


Fig. 5. Relationship between shell length and terminal velocity of black mussels dropped through air.



function of the falling object's shape and mass. Figures 2–4 illustrate various relationships among the physical dimensions of black mussels.

The terminal velocity of mussels was determined in a wind tunnel, in which mussels of known size were mounted individually on a sting. Wind-tunnel speed was calibrated from the difference in the static and dynamic head of a pitot tube. The terminal velocity was given by that wind velocity which exactly opposed the gravitational attraction on the mussel and caused it to remain suspended in the wind-tunnel. Figures 5 and 6 show the observed relationships between velocity, size of mussels, and drop-height.

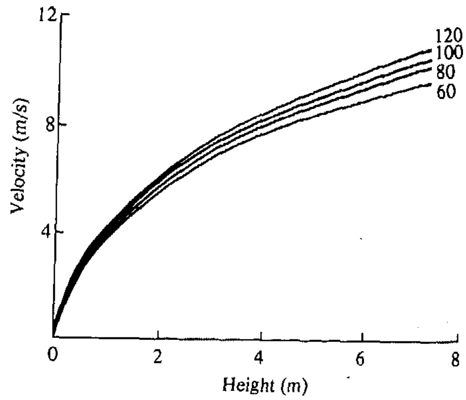


Fig. 6. Relationship between drop height and impact velocity of black mussels of various lengths (indicated in mm against each curve).

The fracture stress of the mussels was determined by means of a free-swinging pendulum in the form of a smooth steel plate, which was arranged to strike the lightly-held mussel from progressively greater heights of release. For the impact test the specimen was mounted 'sideways on', since it was noted that mussels dropped into a tank of water invariably landed at the bottom on the anterior adductor scar region of the shell, quite independently of the position in which they were released. Figure 7 shows the relationship between mussel mass and the height from which the pendulum had to be released to cause fracture. There was an indication that a relatively greater force was needed to fracture small mussels. The main conclusion, however, was that all mussels, no matter what size or mass, fractured when subjected to an impact velocity corresponding to a pendulum height of about 1 metre.

In order to simulate natural conditions, mussels were dropped from increasing heights until their shells broke. They were

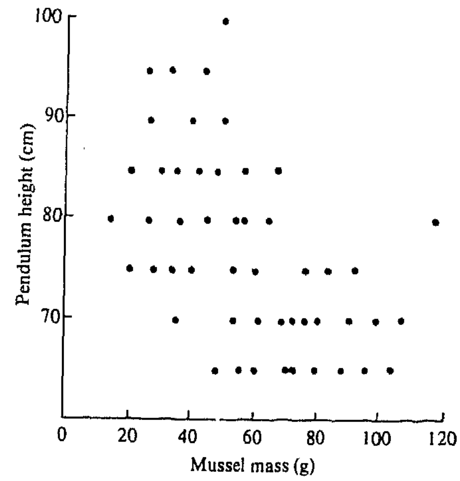
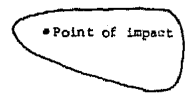


Fig. 7. Relationship between whole-body mass of black mussels and pendulum height required to cause fracture of shells. The pendulum bob was of mass 2.5 kg, the supports being of negligible mass. The equipment was arranged so that the impact surface struck the lightly supported mussel at the point of maximum descent of the pendulum, and on a line with the centre of gravity of the pendulum bob. The experimental mussel was orientated so that it was struck as indicated in the diagram.



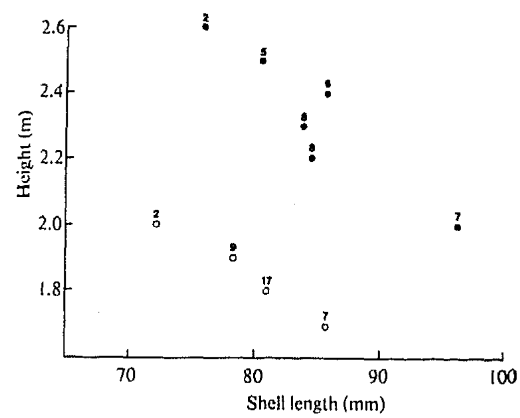


Fig. 8. Relationship between shell length and drop height of black mussels which fractured on smooth concrete (open circles) and a tarred surface (solid circles). The figures represent numbers of mussels dropped.

Table 4. Success of mussel-dropping behaviour in relation to distance (m) separating adult kelp gulls at sandy or rocky drop-sites.

	10-m intervals between potential pirate gulls and drop-site				
	0–9.9	10–19.9	20–29.9	30–39.9	40–100 m
Sand					
No. drops successful first time [a]	4	2	2	4	1
No. drops unsuccessful first time [b]	14	9	7	5	3
No. drops unsuccessful due to pirating by other gulls	7	0	0	0	0
No. drops observed	25	11	9	9	4
Rock					
No. drops successful first time [a]	20	14	4	5	4
No. drops unsuccessful first time [b]	13	2	0	0	0
No. drops unsuccessful due to pirating by other gulls	14	0	0	0	0
	47	16	4	5	4

[a] Mussel shell cracked and gull fed on contents. [b] Mussel shell failed to crack sufficiently for gull to feed.

dropped onto a tarred road or onto a smooth concrete floor (Fig. 8). All mussels fractured on concrete when dropped from above 1.7 m; on a tarred surface they fractured when dropped from above 2.0 m. As in the pendulum experiment, there was an indication that relatively greater heights were necessary to fracture small mussels. The overall conclusion from these tests was that the shells of fresh black mussels, dropped from heights between 1 and 2 m, or attaining velocities in the range 3.4–6.0 m/s, generally fractured on impact with hard surfaces.

Heights from which gulls drop black mussels

The behaviour of gulls in dropping fresh black mussels, 80 mm long, was recorded by ciné camera. A stopwatch was used to time the fall of the mussels and the subsequent descent of the gulls. Drop-time was converted into drop-height with the aid of a standard curve (Fig. 9).

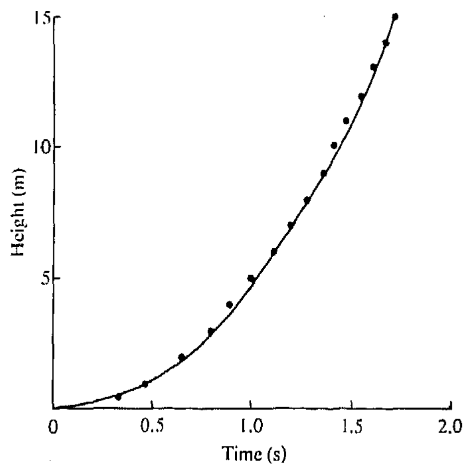


Fig. 9. Time taken by an 80-mm black mussel to reach the ground when dropped from different heights.

The drop-sites were categorized as sand, large areas of relatively flat rock (including concrete breakwaters), and small areas (<10 m^2) of jagged, broken rock surrounded by sand. A significant difference in the height from which mussels were dropped was found between two of the three categories (Table 3). Adult gulls which dropped mussels onto sand tended to fly highest before releasing their prey, whereas adult birds which used areas of flat rock tended to ascend the least. It has not yet been proven, however, that individual birds actually adjust their drop-height depending on substrate. The fact that gulls tended to ascend highest when releasing mussels over sand might be considered a reflection on the inexperience of the birds concerned. However, if that were so then one might expect an equal tendency for the birds to drop mussels from relatively low elevations, which was not the case (Table 3). There was a small, but not statistically significant, difference in the drop-heights of gulls using the two different rocky substrates (Table 3).

Individual kelp gulls evidently become highly skilled in dropping mussels. An artificially-marked adult presented consecutively with 20 standard-size (80 mm) mussels made 21 drops of which 19 were successful (fractured sufficiently for the bird to extract the meat) at first attempt. This bird dropped mussels onto a concrete breakwater, and operated at heights spanning a relatively small range (x = 3.9 m [3.9–4.5 m], n = 18).

The data in Table 3 pertain to birds which dropped mussels while 50 m away from any other gulls, when the risk of piracy or any other form of interference was negligible. Theft occurred frequently when a gull dropped a mussel within 10 m of another (Table 4). Those gulls which dropped their mussles farther than 10 m from conspecifics did not lose their

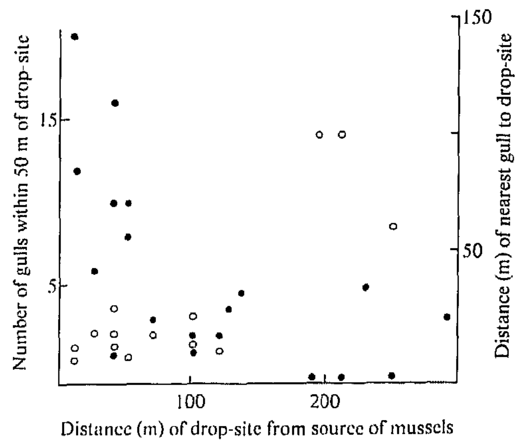


Fig. 10. Relationships between number of kelp gulls (solid circles) within 50 m of a sandy drop-site, distance of nearest gull to drop-site (open circles), and distance separating the sandy drop-site from the source of black mussels.

prey to pirates, and the overall success rate of gulls dropping mussels on rock went up with increasing distance between themselves and other gulls. Within a 10-m radius of the drop-site, the mean distance separating pirates and pirated gulls was 3.8 m (S.D. 1.2 [2–5 m], n = 7) and 2.9 m (S.D. 1.6 [1–6 m], n = 14) for sandy and rocky sites respectively. Mean nearest-neighbour distance between all mussel-dropping birds and conspecifics was 4.8 m (S.D. 1.6 [2–8 m], n = 25) and 3.7 m (S.D. 1.9 [1–9 m], n = 47) for sandy and for rocky sites respectively, within a 10-m radius of the site.

Along a stretch of beach where sandy and rocky areas alternated in close proximity (<0.25 km apart), a total of 25 adult gulls gathered within a 50-m area where mussels were stranded at low tide. Those birds which dropped their prey farthest from the 50-m boundary of the initial point of collection encountered fewest potential pirates at the drop-sites and also tended to be farthest removed from a potential pirate. The potential risk of interference apparently was lowest for those birds which chose to drop their prey onto sand (Figs 10 and 11).

Time taken by a gull in recovering its prey

After releasing a mussel, a gull should descend to the ground to recover its prey as quickly as possible, to prevent piracy by other gulls. Gulls which dropped mussels onto sand took significantly longer ($p < 0.05$, F-test) to recover their prey than

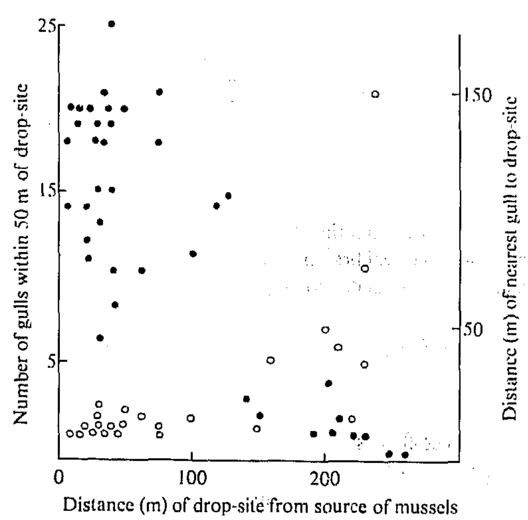


Fig. 11. Relationships between number of kelp gulls (solid circles) within 50 m of a rocky drop-site, distance of nearest gull to drop-site (open circles), and distance separating the rocky drop-site from the source of black mussels.

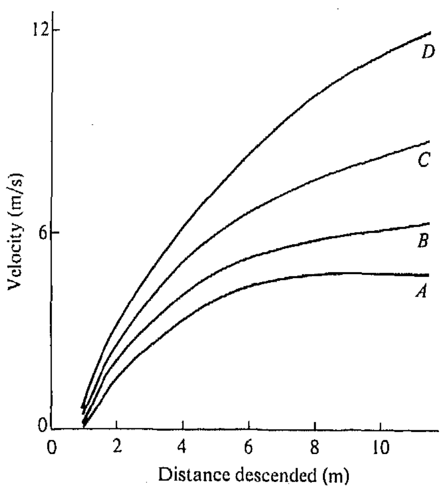


Fig. 12. Velocity of a descending kelp gull as a function of distance descended, with wings fully open (*A*), wings two-thirds open (*B*), wings one-third open (*C*), and wings fully closed (*D*).

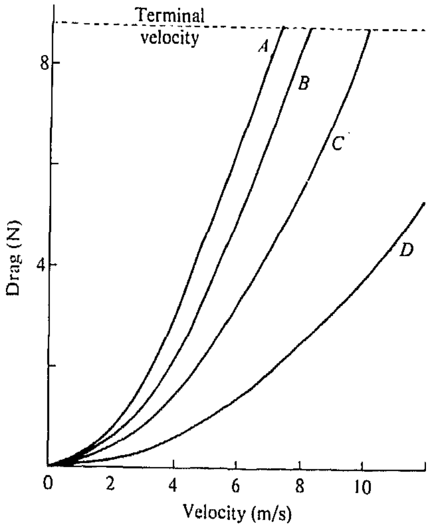


Fig. 13. Relationship between drag and velocity for a descending kelp gull; wings fully open (*A*), wings two-thirds open (*B*), wings one-third open (*C*), and wings fully closed (*D*).

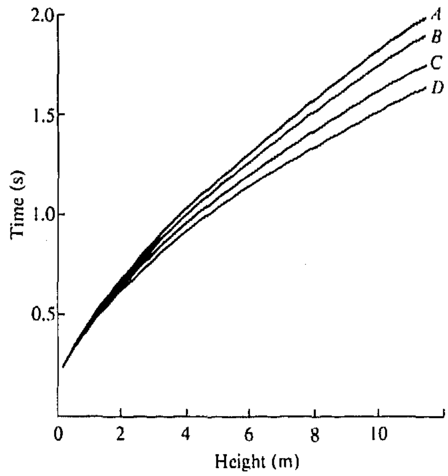


Fig. 14. Time taken by a kelp gull to reach the ground after descending from different heights; wings fully open (*A*), wings two-thirds open (*B*), wings one-third open (*C*), and wings fully closed (*D*).

those which used rocky drop-sites (Table 5). The mean recovery time (1.33 s, $n = 14$) for juvenile gulls was significantly longer ($p < 0.01$) than for adults (1.0 s, $n = 29$) over sand.

The mass of a kelp gull is approximately 0.9 kg. Terminal velocity of the gull is reached when the drag (D) is equal to the bird's weight, that is, $D = 9.81 \times 0.9$ N. Terminal velocity is given by

$$V = \sqrt{D/0.5\, \rho A C}$$

where p is the density of air (1.22 kg/m^3), C is a friction term (estimated to be 1.5 for a gull's wing, compared with 1.2 for a disc and 1.7 for a plate), and A is the bird's total surface area (estimated to be 0.19 m^2; one wing = 0.075 m^2, body = 0.04 m^2). The time taken by a gull to reach the ground from whatever height can be deduced from the relationships illustrated in Figs 12–14.

Figure 14 shows that theoretically a gull descends at a speed of about 4 m/s compared with 5 m/s for an 80-mm mussel (Fig. 9). This means that a gull which released a mussel from a height of 10 m would reach the ground 0.5 s later than its prey. The actual descent of the gull was somewhat slower than that predicted by the model. Actual mean recovery time was 1.0 s (0.7–1.4 s, $n = 7$) for adult gulls which descended from 10 m onto sand. This was because the bird slowed itself down, by flapping its wings, to control its velocity before coming to land. The incidence of wing-flapping during descent was apparently related to wind velocity, which was not measured. Gulls tended to orientate themselves into the wind when dropping mussels.

Table 5. Average time (s) for descent of kelp gulls after releasing black mussels and average time (s) mussels are on ground before retrieval by their 'owners'. Further particulars in Table 3.

Sand		Jagged rock		Flat rock	
Gull's descent	Mussel on ground	Gull's descent	Mussel on ground	Gull's descent	Mussel on ground
2.5	1.14	1.68	0.79	1.48	0.66
S.D. 0.53	S.D. 0.38	S.D. 0.34	S.D. 0.25	S.D. 0.36	S.D. 0.26
(1.4–4.2)	(0.5–2.1)	(1.0–2.4)	(0.4–1.3)	(0.9–2.2)	(0.2–1.3)
$n = 30$	$n = 30$	$n = 22$	$n = 22$	$n = 18$	$n = 18$

Conclusion

The work reported here forms part of a general study of the kelp gull's predatory behaviour. Preliminary results indicate that the species is a highly adaptive food generalist, but individuals tend to specialize in making maximum use of particular foraging techniques. It is apparent that the mussel-dropping behaviour of the kelp gull varies considerably, but the precise conditions which influence this variation are not obvious. Barash *et al.*[2] speculated on some of the factors involved in the differences which they observed in the form and efficiency of clam-dropping behaviour by glaucous-winged gulls *Larus glaucescens*, and much of their reasoning apparently can also be applied to the kelp gull. In particular, social status as much as level of learning could be important in influencing the mussel-dropping behaviour of individual birds.

Individual kelp gulls which prey on mussels apparently employ individual strategies which differ in form but need not necessarily differ in efficiency of operation. It is therefore difficult to answer the question: what constitutes a superior performance in mussel-dropping behaviour? Since the height from which the mussel is dropped is only one of the factors involved, there is no simple answer to the question: what is the optimum height from which a kelp gull should drop a black mussel? However, depending on local circumstances, use of a flat, hard substrate appears to make for maximal efficiency, and large black mussels normally break when dropped from 1.5 m onto such a substrate. Seemingly, few kelp gulls attain this level of proficiency.

In future observations, it would be interesting to learn whether gulls adjust drop-height in accordance with differences in type of mollusc (not only black mussels are dropped) and, if so, what cues the birds use in distinguishing between molluscs in respect to both size and species.

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