Drop-catch behaviour is play in herring gulls, *Larus·argentatus*

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Behaviours with no apparent adaptive function are sometimes described as play without rigorous testing of alternative explanations. One such behaviour is the repeated dropping and catching of objects by birds. We observed drop-catch behaviour by herring gulls over 3 years at a site where the birds frequently dropped clams to break them on hard surfaces below. We tested unique suites of predictions from three hypotheses, that the drop-catch behaviour is play, that it functions to expose potential kleptoparasites, or that it serves to reposition clams before foraging drops. We tested data from 72 drop-catch series and 504 typical foraging drop series to determine which suite of predictions most closely matched our observations. As predicted if the behaviour were play, drop-catches were performed more by younger birds, not necessarily over a hard substrate, and sometimes with nonfood objects. Clams that were subjected to drop-catches were generally not repositioned or eaten. These results suggest a motivation for drop-catching that is distinct from foraging. Finally, drop-catches were more frequent when it was warm and when there were high winds, also consistent with the play hypothesis. Drop-catch behaviour closely matched the predictions of the play hypothesis and we were able to reject the two alternative explanations.

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Herring gulls often forage on clams by dropping them onto hard surfaces such as asphalt roads to crack the shell (reviewed in Cristol & Switzer 1999). Occasionally, rather than letting clams drop, gulls attempt to catch them before they hit the ground (hereafter, drop-catch behaviour). Similar behaviour has been labelled play in this and other gull species (e.g. Humphreys 1964; Terry 1990; Wheeler 1943). However, most such reports are anecdotal and do not provide a rationale for classifying the behaviour as play. In fact, play is often used as a largely untested default explanation when an observer forms the subjective opinion that a given behaviour has no immediate function (Martin & Caro 1985).

Because there are so many forms of play the definition is necessarily broad. One commonly cited definition is 'apparently purposeless activity with no immediate adaptive goal, utilizing species-typical motor programs that are exaggerated in intensity or number of repetitions, or misordered compared to mature behaviour, or mixed together with behaviour appropriate to different contexts' (Gould & Gould 1994, pp. 164–165). This generality has made it easy for researchers to dismiss any enigmatic behaviour as play without rigorous testing. One example

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of such a behaviour is the drop-catch performed by gulls, which is repetitive, utilizes motor programmes typical of gull foraging behaviour, and seems to serve no immediate adaptive goal.

Play is rarer among birds than mammals, possibly because elevated body temperature, small size, and high activity lead to greater metabolic stress and lower energy reserves in birds (e.g. Barber 1991; but see Gould & Gould 1994, page 165). Of the three categories into which play behaviour is normally divided, social, locomotor and object, birds are most often reported to engage in object play, that is, activity directed towards an inanimate object (Ficken 1977; Ortega & Bekoff 1987). This involves manipulating, but not eating, objects found near the bird such as leaves, twigs, stones, or prey (Gould & Gould 1994, page 165). Both locomotor and object play have been reported in members of the avian order Charadriiformes, which includes gulls (Ortega & Bekoff 1987).

Our objective in this study was to test three proximate explanations for the function of an unusual behaviour that has been described as play in the past without rigorous testing (e.g. Graham 1988; Warden. 1982). We tested the hypothesis that drop-catch behaviour by gulls is play. We also tested two alternative hypotheses to explain the dropping and catching of prey. In the kleptoparasite detection hypothesis, the drop-catch is explained as allowing the gull dropping a clam to

Table 1. Predictions of the play, kleptoparasite detection and repositioning hypotheses for drop-catch behaviour and observed results*

	Play	Kleptoparasite	Repositioning	Observed
(1) Are drop-catchers young?	**Yes**	?	?	Yes
(2) Are soft substrates used?	**Yes**	No	?	Yes
(3) Are only clams dropped?	**No**	Yes	Yes	No
(4) Is the clam eaten?	No	Yes	Yes	No
(5) Is the clam repositioned?	No	No	**Yes**	No
More frequent when:				
(6) Other gulls are nearby?	Yes	**Yes**	?	No
(7) Temperature is warm?	Yes	No	?	Yes
(8) Wind speed is high?	Yes	No	?	Yes

*__Boldface__ indicates critical prediction(s) of each hypothesis. Question marks indicate cases in which there was no basis for a prediction. See text for statistical analysis of observed results.

determine whether nearby gulls are attentive and move towards the drop site when the clam is released. A gull could thereby test the likelihood of theft without relinquishing control of a clam. If other gulls moved towards the spot where the clam would have landed, the dropping gull could select a different site after catching the clam. The other alternative explanation, the repositioning hypothesis, posits that the drop-catch is an attempt to reposition the clam in the gull's beak in order to better orient it for a drop onto a hard surface to break it open. This assumes that (1) certain orientations lead to a greater probability of cracking upon impact, and (2) on occasion, gulls extract clams from the mud and begin flying before orienting them appropriately in the beak, or lose their grip while flying. Each of the three hypotheses makes a unique suite of predictions (Table 1).

Predictions

Play hypothesis

(1) A higher proportion of the drops performed by juveniles will be drop-catches than the proportion performed by older gulls. Young animals typically play more frequently than adult animals, possibly because altricial young do not have to devote time or energy to finding food or protecting themselves (Bekoff 1984; Hall 1998; Ortega & Bekoff 1987).

(2) Drop-catches will occur more often over soft substrates than will foraging drops. Foraging birds aim specifically at hard surfaces to break the clam's shell (Gamble 2000, page 12), while playing birds, which would not be motivated to crack the shell, would not require a hard surface.

(3) The object dropped will be a clam less often in drop-catches than in foraging drops. While foraging drops should only involve clams, both clams and novel items will be used in play (Pellis 1981; Wood-Gush & Vestergaard 1991).

(4) The clam will not be consumed at the end of a drop series involving a drop-catch as often as at the end of a drop series involving only foraging drops. The motivation for play differs from the motivation for foraging; object play involves manipulation rather than eating (Pellis & Pellis 1998). Although motivation might be expected to change over the course of a long play sequence, a series of drop-catches typically lasted less than 30 s, making it unlikely that the motivation would change to hunger.

(5) The drop-catch will not lead to the repositioning of the clam more often than expected by chance. Herring gulls nearly always carry clams with the wide end (umbo) facing away from the mouth. If drop-catches are a form of play, gulls will return the clam to the same position or reposition it randomly. In neither case would the clam be repositioned by the end of a drop series significantly more than half the time.

(6) The drop-catch should be performed more, relative to foraging drops, when the number of other gulls nearby increases. Object play is stimulated in both kittens and monkeys by the presence of other individuals (Egan 1976; Menzel 1976). Although the effect of other individuals may not be as dramatic in gulls, since they are less social than kittens or monkeys, several studies have shown that various kinds of play increase in the presence of other individuals (Baldwin & Baldwin 1974; Cheney 1978; Einon et al. 1978).

(7) A higher proportion of drop-catches, relative to foraging drops, will be performed on warm days when gulls are not cold-stressed. Poor weather or food shortage limits play because animals need to conserve energy (Bateson et al. 1990; Fagen 1982). During our study, temperatures rarely reached the lower critical temperature of the typical bird's thermoneutral zone (Calder & King 1974); therefore, the prediction of a positive relationship between temperature and drop-catches should hold for all temperatures at which we observed gulls.

(8) Drop-catches will occur at higher average wind speeds than foraging drops. A bird performing a foraging drop, in which maximum control would be desirable, should drop during lower winds, while a playing bird

should take advantage of high winds, which make flight less expensive (Beck 1982).

We consider predictions 1–3 to be critical predictions of the play hypothesis. Predictions 4 and 5 are strong predictions of the play hypothesis. Predictions 6–8 are weaker predictions than the others due to uncertainties concerning the costs of play at different levels of these variables. For example, high winds significantly reduce the cost of flight in some birds (Furness & Bryant 1996), but we do not know the specific effects of wind speed on the energetics of a drop-catching gull.

Kleptoparasite detection hypothesis

(2) The drop-catch will occur, on average, over the same hard substrate as the foraging drop. Detection of kleptoparasites should occur over an area on which a foraging gull would drop a clam.

(3) The object dropped will always be a clam, since the motivation is to eat the dropped object after testing for the presence of kleptoparasites. The motivation for drop-catching is the same as for foraging, namely, hunger. Thus only clams should be dropped, as in foraging.

(4) The clam will be consumed at the end of a drop series involving a drop-catch as often as at the end of a drop series involving only foraging drops. If drop-catches are a component of foraging, then gulls should end drop-catch series with a normal foraging drop resulting in a cracked clam.

(5) The drop-catch will not lead to the repositioning of the clam more often than expected by chance. (As explained for prediction 5 of the play hypothesis.)

(6) Drop-catches will occur a greater proportion of the time, relative to foraging drops, when more potentially kleptoparasitic gulls are near the drop site. Gulls feeding alone should not waste time testing whether potential kleptoparasites are present. It should be noted that kleptoparasitism was frequent at our study site throughout each winter and gulls rarely dropped clams without some threat of kleptoparasitism.

(7) Drop-catches will be performed more often in low temperatures, since they are a component of foraging. Gulls need extra energy for thermoregulation during periods of extremely cold weather and therefore should have greater motivation to prevent their clams from being stolen by other gulls.

(8) More drop-catches will be observed at lower average wind speeds. Clams will become more valuable at low wind speeds because flight will be more expensive and thus the motivation to avoid being kleptoparasitized will be greater. While gulls have a metabolic rate of only twice their resting value when gliding, they have a value of six to eight times their resting value when engaging in horizontal flapping flight, and even more energy is required for ascending flapping flight (Phillips et al. 1985, pp. 25–27). Therefore, as wind speed increases and birds can rely more on gliding flight, they will have to expend less energy than they would in flapping flight.

We were unable to derive a prediction with regard to the age of the drop-catching gull, because we do not know whether old or young birds would be more reliant on kleptoparasite avoidance behaviour. Prediction 6 is the critical prediction of the kleptoparasite detection hypothesis. Predictions 2–5 and 7 are strong predictions of the kleptoparasite detection hypothesis. We consider prediction 8 to be weaker than the others because of uncertainties regarding flight cost and the magnitude of its effect on kleptoparasitism risk.

Repositioning hypothesis

(3) The object involved in the drop-catch will always be a clam. No other prey items of the herring gulls at our study site require dropping to break hard shells.

(4) The clam will be consumed at the end of a drop series involving a drop-catch as often as at the end of a drop series involving only foraging drops. The purpose of the drop-catch is to orient the clam in a way that will allow it to crack more easily when it is dropped and hunger is the motivation for the drop-catch.

(5) The critical prediction is that the clam will be repositioned in the gull's beak at the end of a series of drop-catches more often than expected by chance (P>0.5). If gulls are drop-catching to change a clam's orientation in the bill, they will only do so with clams that are improperly oriented, and thus at the end of a drop-catch series a clam's orientation should have changed more often than expected if gulls are drop-catching for other reasons. If gulls are not drop-catching to reposition prey, clams would either (1) never be repositioned, because they were already in the proper orientation, or (2) be repositioned half of the time if orientation is irrelevant. The repositioning hypothesis predicts a repositioning rate significantly higher than 50%, although perhaps lower than 100% if repositioning is difficult or not of great value.

Predictions 3 and 4 are strong predictions of the repositioning hypothesis, which provides no predictions regarding age, substrate, number of other gulls, temperature, or wind speed (see Table 1).

METHODS

Study Site

Herring gulls drop and consume approximately 10 000 clams (*Rangia cuneata*) each winter from the mudflat created at the confluence of the Powhatan Creek and the James River, James City County, Virginia, U.S.A. (unpublished data). During most low tides, extensive mudflats are exposed adjacent to a paved road, allowing access to

both clams and a hard surface for breaking their shells. Approximately 25–50 herring gulls were present on the mudflat at any given low tide. Gulls of all age classes (determined by plumage colour) used the site, with approximately equal numbers of yearling and mature (>3 years old) individuals, and small numbers of intermediate-aged birds present every day (on a typical census 20% of all birds were 2–3 years old). Up to 250 gulls of four other species were present at all times at the site as well, but because none of them foraged on clams or attempted to steal clams from dropping herring gulls, we did not include data from other species in this study.

Data Collection

We observed herring gulls for approximately 80 h on 38 days for 1–3 h surrounding low tides from after their annual migration to the site in late November through their departure in late March or early April in 1997–2000. We recorded air temperature and wind speed every 15 min using an Ultimeter 100 weather station. We collapsed temperatures and wind speeds into 5°-Fahrenheit (later converted to Celsius) and 5-km/h categories, respectively, which provided approximately equal sample sizes of drops in each category. We recorded the age (1, 2, 3, >3 years old) and number of herring gulls present every 30 min. Each data point consisted of a behavioural sequence that began with a gull acquiring a clam and ended with loss or consumption of the clam after dropping. We recorded the type of drop (normal foraging drop or drop-catch) and the substrate type over which the object was dropped (asphalt, grass, water, mud, or rock). A pebble- and shell-covered artificial island (area=24 m²) was located on the mudflat 140 m east of the road and was the only hard substrate available other than the road. We noted the number of gulls of any age within 5 m of the drop site each time a drop occurred. On the artificial island, which was usually covered with loafing gulls, we only recorded the number of gulls within 2 m of the drop site because those farther away could not kleptoparasitize a clam dropped into such a crowd. We also noted the identity of the dropped object (e.g. stick, shell fragment, whole clam), its fate at the end of the drop series (abandoned, stolen, or eaten), and whether it was repositioned from before the first drop-catch to after the last drop-catch in a series.

Statistical Analyses

To avoid one form of pseudoreplication, only the first drop in a series of drops performed with the same clam was used in the analysis. We believe that a large number of different individuals used the site because (1) the adjacent James River is a roosting site for many thousands of gulls, (2) individuals with recognizable characteristics were rarely seen more than once, and (3) the data were gathered in 14 different months over a 3-year period. However, we did not mark individuals so we do not know how many different birds contributed to the data set. In Fig. 1 we present results as number of drop-catches
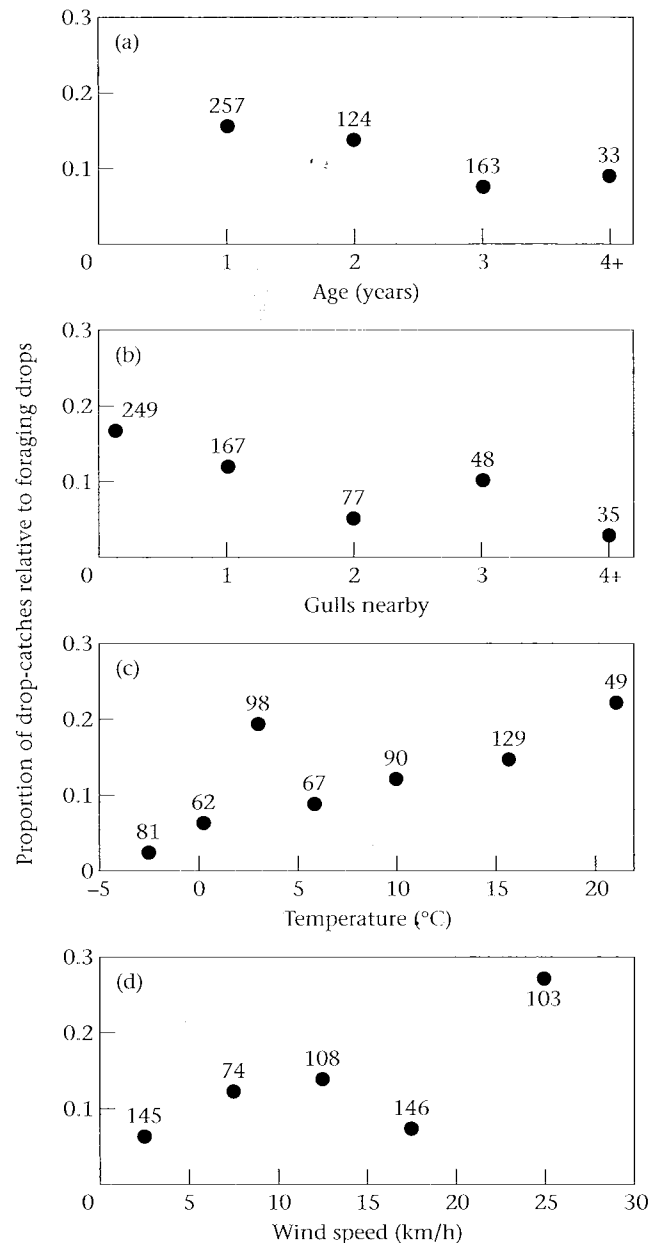

Figure 1. Relationship between proportion of drop-catches, relative to foraging drops, and (a) age, (b) number of gulls nearby, (c) temperature and (d) wind speed. Numbers above data points indicate sample sizes of drops.

divided by number of typical foraging drops seen under the same circumstances to control for changes in rates of feeding, numbers of gulls, or other factors that might affect the absolute number of drop-catches observed. We compared groups using chi-square tests on drop-catch frequencies relative to frequencies of normal foraging drops. In the comparison of drop-catch frequency by age groups we lumped drops by third-year and older gulls because of low sample sizes for older gulls and the possibility of occasional misclassification of cryptic third-year gulls as older birds. We observed few drops with more than four gulls nearby, so we lumped all such cases into one category and compared it to drops with zero,

one, two or three other herring gulls nearby. In the comparison of drop-catch frequency to temperature, we lumped the six highest 5°-temperature categories into three 10°-categories to increase sample size in each. In cases with more than two levels of the independent variable, when a significant difference was found across all categories we performed a post hoc comparison of the lowest versus the highest level of the independent variable. Statistical power was calculated for nonsignificant results (Cohen 1969).

RESULTS

Consistent with the play hypothesis, younger birds performed a higher proportion of drop-catches (chi-square test: χ^2_2=6.4, P=0.039; Fig. 1a). A post hoc comparison revealed a significant difference between the frequency of drop-catches performed by the youngest and oldest gulls (chi-square test: χ^2_1=5.1, P=0.024). As predicted by the play hypothesis and contrary to the kleptoparasite detection hypothesis, drop-catches were more commonly made over soft substrates (40% of 146 drops) than were foraging drops (3% of 430 drops) (chi-square test: χ^2_1=94.8, P<0.0001). Consistent with the play hypothesis, but not the other two hypotheses, birds were less likely to perform a drop-catch when carrying a clam (9% of 542 drops) than when in possession of a nonclam (62% of 34 drops) (chi-square test: χ^2_1=80.2, P<0.0001). Also consistent with the play hypothesis, but not the other two, clams that were eaten at the end of a drop series had been involved in drop-catches significantly less often (<1% of 297 drops) than clams that were not eaten at the end of a drop series (19% of 258 drops) (chi-square test: χ^2_1=49.7, P<0.0001). The critical prediction of the repositioning hypothesis was that clams would be reoriented more than 50% of the time to facilitate easier opening. We observed that clams were reoriented by the end of only 30% of drop-catch series. We thus failed to reject the null and can reject the repositioning hypothesis (chi-square test: χ^2_1=1.0, P=NS), but in only 13 cases could we determine clam position both before and after a drop-catch series, so our chance of rejecting the null was low from the outset (statistical power of approximately 10% for 'small' effect size and 40% for 'large' effect size; Cohen 1969, page 228). Contrary to the critical prediction of the kleptoparasite detection hypothesis, and a weak prediction of the play hypothesis, the proportion of drop-catches decreased as the number of gulls nearby increased (Fig. 1b). Note that this result was in the direction opposite that predicted by either hypothesis (chi-square test: χ^2_4=11.3, P=0.02). As predicted by the play but not the kleptoparasite detection hypothesis, we observed a higher proportion of drop-catches at higher temperatures (chi-square test: χ^2_6=19.6, P=0.003; Fig. 1c). A post hoc comparison revealed a significant difference between the frequency of drop-catches during the warmest and coldest temperature intervals (chi-square test: χ^2_1=10.7, P=0.001). As predicted by the play hypothesis but not the kleptoparasite detection hypothesis, drop-catches were more frequent at higher wind speeds (chi-square test: χ^2_4=29.0, P<0.0001; Fig. 1d). A post hoc

comparison revealed a significant difference between the frequency of drop-catches performed during the highest and lowest wind speed intervals (chi-square test: χ^2_1=15.1, P<0.0001).

DISCUSSION

Consistent with the play hypothesis, younger gulls performed the drop-catch more often than older gulls. In addition, the drop-catch was performed over soft substrates more often than was a normal foraging drop, suggesting that drop-catches were distinct from foraging behaviour and not related to food acquisition. Gulls carrying a nonclam were more likely to drop-catch it than gulls with a clam, and drop-caught clams were cracked and eaten less often at the end of the drop series than clams at the end of series not involving a drop-catch, both suggesting that drop-catch behaviour is not a component of foraging. The drop-catch did not lead to the repositioning of the clam more often than expected by chance, indicating that the drop-catch does not serve to reorient the clam for a more effective drop. Increasing temperatures and increasing wind speeds increased the chance that a drop-catch would occur, which was predicted because these conditions are favourable for play.

The only prediction made by the play hypothesis that was not supported by the data was that the frequency of drop-catch behaviour would increase as the number of other gulls present at the drop site increased. Even though object play may be performed solitarily, we suspected that the presence of other gulls at the drop site would increase the incidence of play since studies on several species suggest that the presence of others encourages animals to play with objects (e.g. Egan 1976; Menzel 1976). However, this was a weak prediction because most previous studies have been on mammals living in close-knit social groups in captivity, perhaps not an analogous situation to that of migratory gulls foraging in large flocks on the wintering grounds. This finding does allow firm rejection of the kleptoparasite detection hypothesis, since increasing the number of potential parasites nearby should necessarily increase the threat of kleptoparasitism.

Play is thought to have several costs, the most obvious being the energy spent directly on the play activity and the time spent in play that could be devoted to other beneficial activities (Bekoff & Byers 1992). Drop-catch behaviour is consistent with this aspect of play in that more energy is put into performing the drop-catch than a normal foraging drop, due to the extra vertical distance flown. Also, the time spent drop-catching could instead be spent feeding. Another potential cost of play is lowered survivorship due to injuries or increased susceptibility to predation (Harcourt 1991). Although actual predation on drop-catching herring gulls was not observed during our study, eagles harassed gulls frequently during our observations, and the corpses of falcon-killed gulls were found occasionally on the study site.

While the immediate function of the drop-catch as play should be to provide pleasure to the gull, there are several

potential long-term benefits or ultimate explanations for the behaviour. Drop-catching may have been selected for because it allows young gulls to improve the foraging drop used in opening clams through practice of similar motor patterns (Negro et al. 1996; Pandolfi 1996). Alternatively, drop-catching may allow a gull to practice the recovery of a prey item dropped accidentally by itself or another gull, seemingly an important skill for birds that are frequently the subject of midair kleptoparasite attacks. Rather than serving a practice function, drop-catch behaviour might have been selected for because it helps young gulls improve their foraging drop by generally strengthening muscles or establishing neural connections, which could give them greater agility later (Byers & Walker 1995; Fontaine 1994). Alternatively, drop-catching might have been selected for because it encourages exploration, allowing young gulls to learn about potential prey items in their particular environment (Ficken 1977). The observation that nonclams were also dropped is consistent with this idea. Of course, drop-catching may serve more than one of these functions (Thompson 1996). Longitudinal studies on marked individuals will be required to determine whether performing drop-catch behaviour increases a gull's ability to drop clams efficiently or recover pirated clams in midair, and thus whether this form of play may be linked to fitness.

While play has been thoroughly studied in mammals, it has not been well documented in birds. Much of the evidence of play in birds is anecdotal and the more thorough studies have been on only one group, the corvids (e.g. ravens and crows). Beck (1982) conducted a thorough study in which, measuring some of the same variables as those in this study (e.g. wind and substrate), he concluded that the drop-catch behaviour performed by herring gulls was play. However, he did not observe this behaviour in subadult herring gulls other than 1-year-old birds. Also, as in many studies of play, he did not provide or test alternative explanations to the hypothesis that drop-catch behaviour is play. We tested multiple predictions of a play hypothesis based on published research from birds and mammals, as well as the predictions of two alternative hypotheses, the kleptoparasite detection hypothesis and the repositioning hypothesis. Seven of eight predictions of the play hypothesis were supported in contrast to one of seven predictions of the kleptoparasite detection hypothesis and zero of three predictions of the repositioning hypothesis. We have rejected two alternatives to the idea that this behaviour is play, and found results largely consistent with the idea that drop-catch behaviour in herring gulls is a form of object play. Until other alternative hypotheses are proposed, we conclude that this behaviour is play.

Acknowledgments

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