

SIZE SELECTION IN MUSSEL-FEEDING OYSTERCATCHERS

by Bruno Ens

Introduction

From the beginning of September 1980 until the end of November 1980, I studied the social behaviour of mussel-feeding Oystercatchers *Haematopus ostralegus* wintering on the Exe estuary in South Devon (see Goss-Custard et al., 1980). To measure intake rates, mussels *Mytilus edulis* were sampled and weighed and the size of mussels taken was estimated. Enough data were collected to allow some remarks on size selection. Though the resulting story is incomplete, it draws attention to various problems of measurement. I hope it may be of some help in future field studies.

Study area and methods

Observations were carried out from a hide on top of 3 metres of almost portable scaffolding placed on bed 4. The behaviour of ten individually marked Oystercatchers was recorded in a 150 by 150 m part of the musselbed, which was divided into 25 by 25 m sites with bamboo sticks. On 22 and 23 November, 5 samples (each 1/16 m) of mussels were taken per site. All mussels above 17 mm in length were measured and counted. Twenty-five mussels (of a wide size range) were selected per group of 4 sites, to measure ash-free dry weights. In Figure 1a and 1b mean density and mean size of mussels per site are given. The central parts of the bed, which were exposed first, contained the highest densities of mussels (between 500 and 1000 per m²), whereas mean size was smallest. It appears to be generally true, in the Exe estuary, that the parts of the musselbed exposed first contain large numbers of small individuals (Goss-Custard, pers. comm.).

Since the work of Norton-Griffiths (1967) it is well known that Oystercatchers can open their mussels by either hammering or stabbing. However, in this study there were clearly two types of hammering birds:

(a) Ventral hammerers tear a mussel loose from the substrate, carry it to an 'anvil', turn it upside down and hammer at the central part (see Fig.2). When the mussel has cracked, the posterior adductor muscle is severed and the flesh extracted. This is the hammering method described by Norton-Griffiths (1967).

(b) Dorsal hammerers deliver hammering blows sideways or above to a mussel *in situ* and extract the flesh after having severed the posterior adductor muscle (Fig.2). In his pioneering work, Dewar (1908) noted that Oystercatchers opened their mussels in three ways, but I was unable to decide if his classification coincided with mine. He states for instance that (apparently) ventral hammering birds leave their shells undamaged. Norton-Griffiths (1967) showed that individual specializations remained constant and that the inheritance of a particular technique was cultural. In my study most individuals stuck to one method for the entire period. One dorsal hammerer sometimes stabbed and one stabber sometimes hammered dorsally.

When a mussel was captured by an Oystercatcher the length was estimated, to the nearest ½ cm., by comparing it with the known length of the colour-bands. This was always possible with my only ventral hammering individual, henceforth called Bella. For other individuals size could only be estimated if the Oystercatcher carried its mussel over a short distance or fed close-by.

Problems in measuring the size of mussels taken

The accuracy of this estimation method was checked on one occasion by later retrieving the mussels whose length I had estimated. The mussels were located with the aid of a detailed map of all nearby pools. In 25 out of 30 cases the estimated length was within half a centimetre of the real length (Fig.3). The two outliers could be due to my recovering mussels opened by another Oystercatcher, although that chance was calculated to be small, as follows. From data on capture rate and bird density, I estimated that there would be an average density of 0.2 captured mussels per m² by the end of the tidal cycle. The position of individual mussels could be pinpointed to an area of about 0.25 m². Assuming that the number of captured mussels per area follows a Poisson-distribution, it can be calculated that only 2% of the areas containing at least 1 mussel would be expected to contain 2 or more mussels.

On several days, as many sites as possible were searched thoroughly to collect freshly opened mussels (with fresh meat attached to the adductor-scar). Collecting shells is probably a reasonably reliable way of measuring shell size in the case of ventral hammerers, because they carry their mussels to 'anvils' on patches of hard sand where they are clearly visible. The estimated size of mussels taken by Bella was similar to the size of ventrally opened mussels collected in the same area (Fig.4). However, collecting shells may introduce a bias against small size-classes in stabbers and dorsal hammerers (Fig.5). The difficulty I had in finding small mussels that I had put down on the musselbed suggests that small ones are less likely to be discerned in a dense cover of mussels. Some evidence for this is presented in Figure 6. The chance of recovery increases with size of mussel, assuming that the estimated size of unrecovered mussels is also biased. Presented this way the effect is not statistically significant ($\chi^2 = 1.28$, $P < 0.10$), but lumping the data in two size classes (big versus small) results in a significant difference ($\chi^2 = 5.17$, $P < 0.05$). Alternatively small mussels may more often be consumed *in situ*, and the carried mussels may be easiest to find (Goss-Custard, pers. comm.). Whatever the reason it seems clear that relying solely on collected mussels in case of stabbers and dorsal hammerers (as done by Drinnan 1958; Goss-Custard et al. 1980; Koene 1978; Norton-Griffiths 1967; Zwarts and Drent 1981) may lead to biased results, although the extent of the bias could vary from place to place, according to the size taken, proportion carried and the nature of the substrate. The bias cannot be attributed to small mussels being swallowed whole (as noted by Evans (1975) for Pied Oystercatchers), because this was never observed to occur.

Problems in measuring the size of mussels present

In this section I discuss two further problems in testing for size selection. Both involve the measurement of the frequency distribution of mussel sizes encountered by the foraging Oystercatchers.

First, I did not measure mussels smaller than 17 mm, so my assessment of the mussels encountered is limited. However, both Hulscher (1964) and Norton-Griffiths (1967) found that small mussels had a high chance of being hidden in the clump, which makes them effectively unavailable. But, in any case, mussels between 15 and 25 mm were rare in my study area.

Second, when the area over which mussels are sampled is large and heterogeneous it may prove difficult to distinguish between patch choice and prey choice. Imagine a hypothetical situation where animals select big prey items because these are most profitable, but mainly forage in sites with small prey because of high prey densities (see Sutherland, in press). Comparison of size taken with size present overall would lead to the 'mistaken' conclusion that the

1

mean density [no/m²]/1000

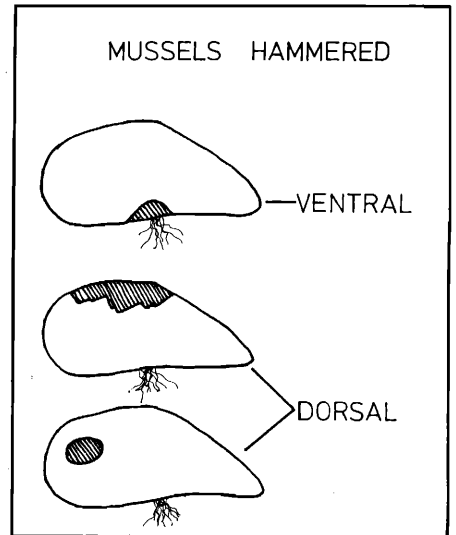
.19	.32	.72	.88	.42	.34
.27	.42	.59	.75	.40	.26
.26	.24	.69	.98	.38	.21
.18	.27	.61	.82	.38	.10
.13	.32	.42	.66	.51	.18
.13	.27	.43	.40	.37	.06

25M

mean size [mm]

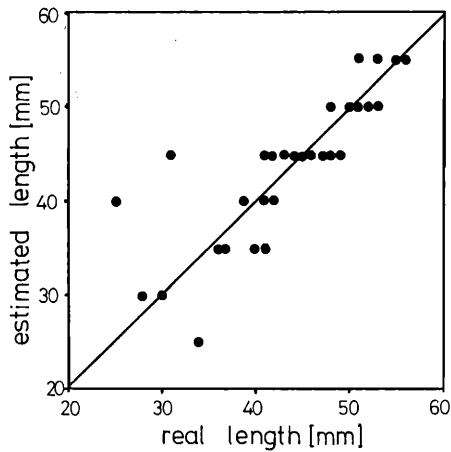
46	45	41	41	41	47
44	42	39	40	42	44
43	41	37	35	41	43
42	41	35	36	37	38
43	41	39	36	39	40
42	43	40	40	42	43

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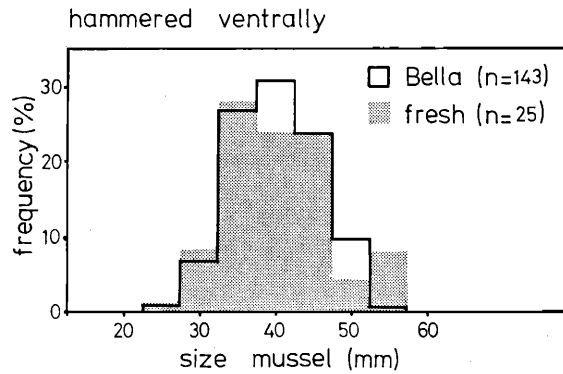


1. Numbers per m² (a) and mean size in mm (b) for mussels greater than 17 mm in the study area.
2. Sites of fractures for mussels opened by dorsal and ventral hammering Oystercatchers. The byssus is drawn to clarify the position of the mussel.

3

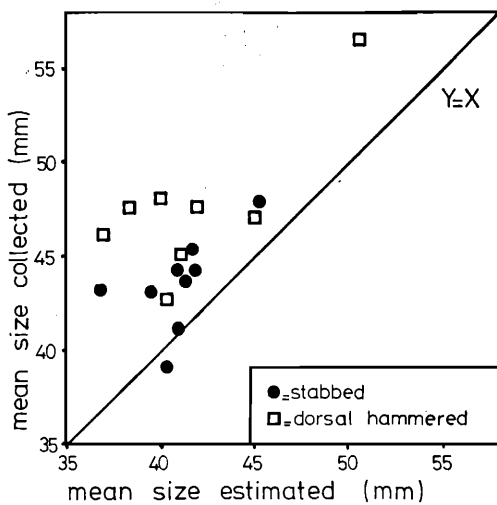


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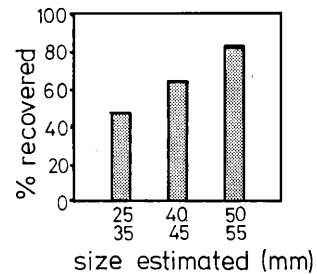


3. Estimated length as a function of real length for mussels opened by the stabber RGB NNB and recovered with the aid of a detailed map of all the tidal pools. The straight line represents correct estimates.
4. Frequency distribution of sizes of mussels taken by Bella and collected freshly opened in the four sites comprising the home range of Bella.

5



6



5. Mean size of collected mussels as a function of mean size for estimated mussels (i.e. taken by one of the focal animals) for dorsal hammerers and stabbers. Every point represents one site. Only sites where more than 5 mussels were collected and where more than 5 mussels were estimated are included.
6. Likelihood of being recovered as a function of estimated size for 45 mussels taken by the stabber RGB NNB during the check on correctness of the estimation method.

hypothetical animals select small prey items from a mixture of large and small. There are several indications that spatial heterogeneity was not a serious problem in this study. Figure 1b shows that mean length changes along a smooth gradient in the study-area. A one-way analysis of variance (36 sites; 5 samples per site; 9 samples containing less than 2 mussels each excluded) revealed significant differences in mean size between sites ($F = 5.24$, $P < 0.000001$). Of the total sum of squares, a major share (58%) was due to variation between sites, leaving 42% to variation within sites. An indication of the absolute magnitude of variability in mean size between quadrats within a site was obtained by calculating standard deviations over the 5 sample means within one site. These standard deviations ranged between 1.0 and 6.8 mm and averaged 2.8 mm. Assuming a normal distribution, this means for instance that if Oystercatchers concentrated all their feeding effort on spots where mean size was more than 2.8 mm (1 standard deviation) greater than the grand mean for the site, they would have used only 16% of the total surface of the site, and this is unlikely. Although individuals sometimes used only the area on the border of their home ranges, it is unlikely the mussels there were either consistently bigger or smaller in size. The population of Oystercatchers as a whole appeared to feed spaced out, probably because they avoided one another (Vines 1980).

To eliminate the problem of patch choice completely, sites smaller than 25 by 25 m² are needed (or a very homogeneous musselbed), but from the above it is unlikely that the analysis is greatly biased this way.

Size-selection by stabbers and dorsal hammerers

Selection occurs if the proportion of a size class taken is different from the proportion of that size present. Ideally, therefore, we should compare the two frequency distributions to test for selection. Since stabbers and dorsal hammerers did not always 'show' their mussels to me (a possible source of bias, by the way) and often spread their feeding effort over several sites, I compared means instead of frequency distributions. This method only detects selection if it is strongly directed at one end of the spectrum of size-classes.

In Figure 7a average size taken is plotted against average size present. Each point represents the data for a site where one individual ate more than 10 mussels. It appears that stabbers and dorsal hammerers prefer big mussels. But this may not be an active preference, but arise through passive selection (Hulscher 1982). This means that the proportion of mussels of different size classes actually found by the bird differs from those present because of the method used to detect them. The problem is to work out for each searching method how mean size present relates to mean size 'encountered' (in the sense of taken notice of).

The assumption of Oystercatchers feeding by touch amidst piles of mussels in daylight may be surprising but some observations point to this. Some stabbers obtained a lot of mussels by probing in the muddy interstices. Dorsal hammerers usually tapped many shells before attacking their final victim. Following Hulscher (1977), studying Oystercatchers feeding by touch on cockles at night, I assume random search. If probing is perpendicular to the mud it is necessary to calculate the surface area (S) of the horizontal cross-section of the mussel. S probably depends on the length (L) in the following way: $S = aL^b$ where a and b are constants. Compared with a mussel of length L_1 , a mussel of length L_2 is $aL_2^b/aL_1^b = (L_2/L_1)^b$ times more likely to be encountered, showing that the value of a need not be known. I have guessed b to be 2 because Hulscher (1977) found this value for cockles *Cerastoderna edule*. To construct the relative frequency distribution of mussel-sizes encountered, the number in every size-class is weighted by the squared length. From this distribution, size encountered is easily calculated.

Although some stabbers hunted by touch, most stabbers clearly hunted by sight, and the majority of their stabs were successful. The derivation of mean size encountered is less straightforward in this case, because we start from less well known empirical relationships. Werner and Hall (1974) showed that the distance (D) over which Bluegill Sunfish *Lepomis macrochirus* detected prey items was positively correlated with the length (L) of these prey items. Plotting their data, I felt that relationship $D = aL$ (where a is a constant) fitted quite neatly. The visual field of an Oystercatcher scanning the musselbed, probably resembles a wedge of a circle. Thus the size of the area (A) in which the mussel is detected becomes proportional to the square length of the mussel: $A = cD^2 = ca^2L^2 = c^1L^2$ where c and c¹ are constants. It is logical to equate the likelihood of detection with the size of the detection area A. Compared with a mussel of length L_1 a mussel of length L_2 is $A_2/A_1 = c^1L_2^2/c^1L_1^2 = (L_2/L_1)^2$ times more likely to be encountered. Direct evidence that passive selection works this way in visual predators is provided by experiments of Joost Tinbergen (pers. comm.), offering captive Starlings *Sturnus vulgaris* small and large pieces of mealworm on a tray. When the size difference was small, the Starlings took mealworms in proportion to their length (which is the same as surface for mealworms cut into pieces).

Thus mean size encountered by Oystercatchers hunting by touch probably equals mean size encountered by Oystercatchers hunting visually in the same area. Plotting average size taken against average size encountered (Fig.7b) shows that the size taken equals size encountered, thus supporting the hypothesis of passive selection.

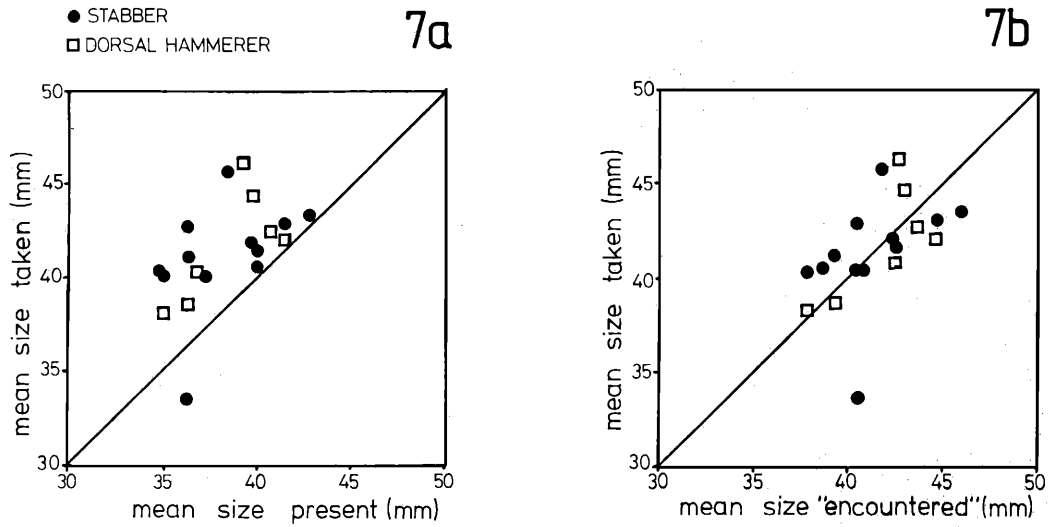
Size selection by ventral hammering Bella and comrades

Ventral hammerers are treated separately because they can be analyzed in more detail: shell collection was unbiased, and Bella restricted her foraging activity to 4 adjacent sites, allowing the comparison of frequency distributions of mussel-sizes. To increase sample size, I treated these 4 sites as one; the frequency distributions of sizes of mussels was very similar. For the same reasons, I lumped the data from the other sites where ventrally hammered mussels were collected, opened by unknown individuals. Comparing size taken with size present (Fig.8) shows selection against very small and very large mussels for both Bella and her comrades. Is this another case of passive selection?

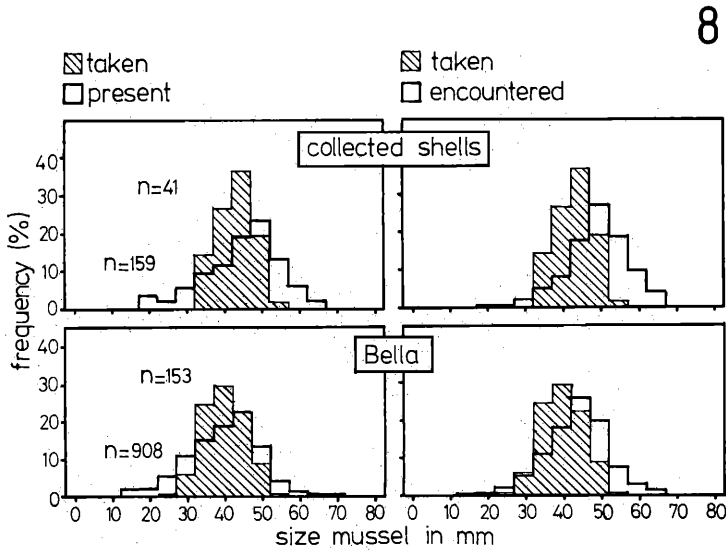
The argument that foraging Oystercatchers encounter a mussel in proportion to its squared length is most compelling for Oystercatchers feeding by touch. Bella always extracted her mussels by probing under patches of seaweed. Comparison of size taken with size encountered (Fig.8) shows even stronger selection against big mussels than before. Selection against small mussels on the other hand might be due to passive selection. However, if ventral hammerers rejected only big mussels, small mussels should be taken in a higher proportion than encountered. This is clearly not the case. Also, of 33 captured mussels smaller than 35 mm, no less than 22 were abandoned by Bella (Table 1). Probably, intermediate sizes are preferred.

Can optimal foraging theory explain Bella's exquisite taste?

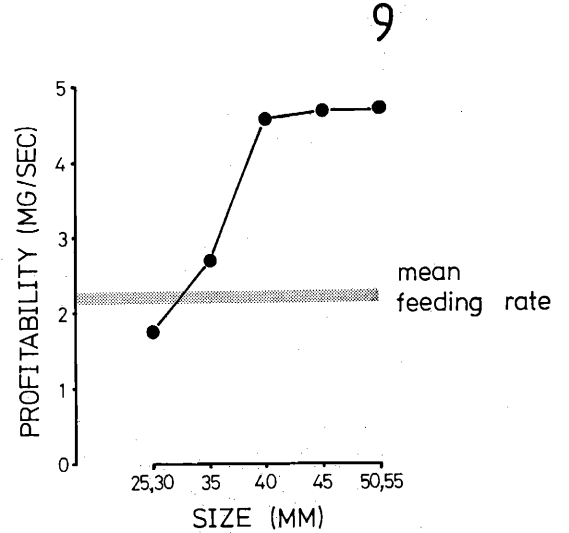
Current models on optimal prey choice, while assuming maximization of intake rate (energy gain per unit feeding time), predict unambiguous decision rules. In a given situation, a predator should either always accept or always reject a specific class of prey items (Krebs 1978). It is predicted that only prey with a profitability (energy gain per unit handling time) equal to or higher than the average intake rate are included in the diet.



7. Mean size of mussels taken as a function of (a) mean size present, calculated as $\frac{1}{N} \sum n_i L_i$, and (b) mean size 'encountered', calculated as $\frac{\sum n_j (L_j)^3}{\sum n_j (L_j)^2}$. Every point represents data on one bird in one site. Only points are included where more than 10 mussels were estimated. The drawn line represents no selection.



8



9

8. Frequency distributions of sizes of mussels taken compared with sizes present (left-hand panel) or sizes encountered (right-hand panel) for Bella (bottom) and collected shells (top).
 9. Profitability (mg AFDW per second handling time) as a function of size of the mussel (in mm) for the ventral hammerer Bella.

Table 1. Calculation of profitabilities per size class of mussels.

A	B	C	D	E	F	G	H	I	J
20	3	100	21						
25	5	80	22)						
)	101	73-130	162	175	1.7	1.1
30	25	60	30)						
35	57	33	40	129	115-143	151	345	2.7	2.3
40	78	42	30	139	122-156	162	634	4.6	3.9
45	64	45	26	173	147-199	196	811	4.7	4.1
50	31	55	26)						
)	160	118-201	193	751	4.7	3.9
55	1	0)						

A. size mussel in mm
 B. number captured by Bella
 C. % of captured mussels abandoned
 D. time (sec) spent per abandoned mussel
 E. handling time (sec) of mussels eaten
 F. 95% confidence limits on handling time
 G. handling time including abandoned mussels
 H. energy content (mg AFDW) of the mussel
 I. profitability excluding abandoned mussels
 J. profitability including abandoned mussels

For each size class, I divided mean ash free dry weight by mean handling time to obtain profitabilities. Since the size of all mussels consumed by Bella could be estimated, calculation of intake rate was straightforward. Bella took smaller mussels than theoretically allowed, but profitability of small mussels was based on few measurements (Fig.9). Bella's 'distaste' of big mussels, however, is very worrying for our theory: the biggest mussels are the most profitable, yet are not selected. Neither can we account for Bella's (feminine?) ambiguity. She abandoned a substantial proportion of mussels of each size class (Table 1).

What has gone wrong?

Given the complexity of the situation in the field, I prefer at present an *ad hoc* hypothesis to rejection of optimal foraging theory. The most likely assumption to be false is that all mussels of one size class are equal in profitability. Some indirect evidence supports this contention. Freshly opened ventrally hammered mussels were hardly ever covered with barnacles, whereas most mussels present were. They seemed slightly less elongated than 'normal' mussels and never showed stunted growth. Sarah Durell (pers. comm.) has noted the same elsewhere on the Exe, as did Paul Koene (pers. comm.) studying a captive ventral hammerer on a Dutch musselbed. It is unlikely that the hammering activity itself should be blamed for the absence of barnacles. Torn-off barnacles leave unmistakable scars. It is tempting to speculate that ventral hammerers specialize on thin-shelled morphs. If true, the shells of abandoned mussels, which can be found on the 'anvils' pressed upside down in the sand, should be thicker than the shells of their less lucky colleagues. Also, the measurements presented here on sizes of mussels encountered and consumed, as well as profitabilities, become irrelevant and have to be done on each morph separately.

Summary

Oystercatchers have three methods to open a mussel: stabbing, dorsal hammering and ventral hammering.

Several problems with field studies on size-selection of mussels by Oystercatchers were identified and discussed:

- Collecting freshly opened mussels may bias against small mussels, in the cases of stabbers and dorsal hammerers.
- If sampling is done over a large and heterogeneous area, no distinction is possible between patch choice and prey choice.
- Probably mussels are encountered in proportion to the surface of their projection.

The case of a ventral hammering Oystercatcher (Bella) was explored in more detail, and it was found that her rejection of big mussels was inexplicable by optimal foraging theory: big mussels were the most profitable. Large variation in profitability within a size class of mussels for ventral hammering Oystercatchers was suggested as a way out.

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