

## FORAGING EFFORT AND PREY CHOICE IN CAPE GANNETS

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In order to test the hypothesis that sardine *Sardinops sagax* are the preferred prey of Cape gannets *Morus capensis*, the link between foraging effort and prey choice was evaluated by simultaneously monitoring the activity and the diet of adult birds attending chicks at Bird Island, Algoa Bay, South Africa. Foraging trip durations were bimodally distributed. Most foraging trips of Cape gannets were completed within 24 h. Metered gannets spent c. 40% of this time flying. In all, nine prey species were recovered from the stomachs of metered birds. The diet was dominated by the commercially important sardine *Sardinops sagax* and anchovy *Engraulis capensis*. Food mass intake by foraging Cape gannets was not correlated with foraging trip duration or time flying, consistent with a patchy distribution of food. Cape gannets returning with sardine tended to have shorter foraging trips and spent significantly less time flying than birds returning with other prey, thereby maximizing net energy intake. Sardine seem to be the preferred (most profitable) prey and, consequently, their relative proportion in gannet stomachs may reflect their absolute availability at spatial scales equivalent to the bird's foraging range.

Seabirds are conspicuous top predators in marine ecosystems and numerous studies have demonstrated that the availability of marine prey can influence aspects of their biology (e.g. Crawford and Dyer 1995). Accordingly, seabirds have been frequently proposed as indicators and predictors of change in populations of their prey (Adams *et al.* 1992, Bost and Le Maho 1993, Montevecchi 1993).

Decadal and interannual fluctuations in diet composition of Cape gannet *Morus capensis*, sampled over most of its breeding range, have been correlated with changes in the abundance of their two main prey species, sardine *Sardinops sagax* and anchovy *Engraulis capensis* (Berruti and Colclough 1987, Crawford *et al.* 1992, Klages *et al.* 1992, Crawford and Dyer 1995). Under conditions when sardine are not overly plentiful, their relative abundance in gannet diet may be predicative of their absolute abundance, measured as fish availability to the local fishing fleet or spawner biomass determined from acoustic surveys (Batchelor and Ross 1984, Berruti and Colclough 1987). Consequently, long-term sampling of the diet of Cape gannets has been rationalized in terms of its potential usefulness as an indicator of the status of local pelagic fish populations (Berruti 1987, Klages *et al.* 1992). That these correlations have predictive power requires a preference ranking of potential prey. To date, this ranking has been based on the physical and biochemical characteristics of the fish prey (Batchelor and Ross 1984). Because of their relatively large size (max. 280 mm standard length) and high energy content ( $8.6 \text{ kJ}\cdot\text{g}^{-1}$ ) compared to alternative prey, sardine are considered

to be the most preferred prey. The superior nutritional value of sardine over Cape hake *Merluccius capensis* has been demonstrated also in a chick-growth experiment (Batchelor and Ross 1984).

Whether or not sardine are preferred prey can be tested by measuring foraging effort in relation to prey choice (Furness and Hislop 1981). Confirmation of field prey preferences of Cape gannets, which integrate the behavioural characteristics of the prey and hence its availability to gannets, will improve interpretation of diet composition data.

On the basis of qualitative and quantitative support for optimal diet choice models (Stephens and Krebs 1986, Kamil *et al.* 1987), it is predicted here that, if sardine are preferred prey of Cape gannets, on foraging excursions in which birds encounter relatively large numbers of them, stomach contents should be dominated by that species. This should be independent of the abundance of other potential prey. Foraging excursions coinciding with low prey availabilities should result in gannets returning with other prey. This paper reports on the field test of the above predictions.

## MATERIAL AND METHODS

### Study site

The study was conducted at Bird Island, Algoa Bay ( $33^{\circ}50'S$ ,  $26^{\circ}17'E$ ), one of the six gannetries along the southern African coast, during November and

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December 1994 and February 1995. The most prominent oceanographic feature of the area is the Agulhas Current, which transports warm, tropical water south-westwards past the south coast of South Africa. Under the influence of the predominant westerly winds, irregular influxes of Agulhas water enter Algoa Bay (Lutjeharms *et al.* 1989) with the associated warm-water fauna, especially in winter (Klages *et al.* 1992). Wind-induced upwelling associated with easterlies may result in sea temperatures dropping to as low as 14°C in summer (Schumann *et al.* 1982, 1988). Upwelling episodes are apparently followed by movement of sardine and anchovy into Algoa Bay, attracted by plankton blooms (Klages *et al.* 1992). As a result of the presence of both warm- and cold-water fauna in Algoa Bay, there is potentially a wider spectrum of prey species available to Cape gannets in this region (Batchelor and Ross 1984) compared with what is available to birds foraging off the west coast of South Africa (Berruti 1987).

#### Measurement of foraging effort

There are technical difficulties in assessing prey availability or abundance at sea over spatial and temporal scales appropriate to foraging seabirds. Accordingly, the foraging effort of Cape gannets themselves was measured as an estimate of prey availability to adult birds attending chicks. Cape gannets search for prey while flying (Nelson 1978), but flapping flight by seabirds is energetically expensive (Birt-Friesen *et al.* 1989, Adams *et al.* 1991). It is assumed here that gannets would minimize flying time during a foraging trip and that this would be a measure of foraging effort.

At least one adult gannet is in attendance at the nest through most of the chick-rearing period. Recently relieved adult gannets were identified by continual observation of a small section of the colony. Such gannets were captured at their nest site using a crooked pole before they departed for sea. The birds were weighed, colour-banded and marked with dye. Finally, an activity meter (see below) was attached. The actual time of deployment of the meter, the activity meter reading and the time of the subsequent departure after release were noted. Subsequently, marked nests were checked at 15-minute intervals from dawn until dusk, recording the time at which the metered gannet was first noted back in the colony. The recently arrived gannet was then recaptured, the time on the activity meter noted and the meter removed. Activity meters were then checked to confirm that they were operating correctly. Stomach contents were retrieved by upending the bird over a bucket and inducing regurgitation. Adult

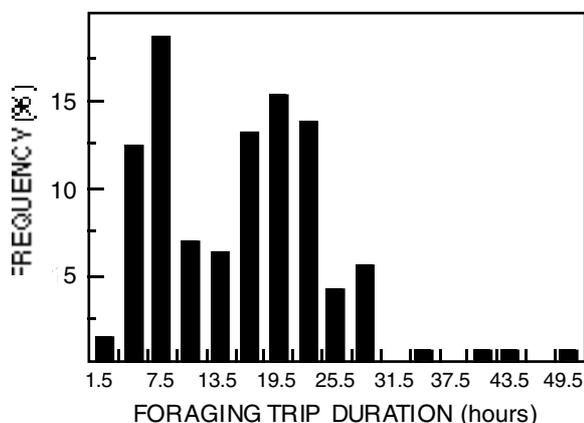


Fig. 1: Relative frequency of occurrence of foraging trip duration of the control group of Cape gannets attending chicks at Bird Island, Algoa Bay

gannets may feed chicks substantial quantities of food within a few minutes of arrival back at the colony. Therefore, if the returning bird was not intercepted before arriving at the nest and transfer of some of its stomach contents had occurred, the chick was also sampled as described for adult birds. In all, 10, 48 and 28 birds were metered in November and December 1994 and February 1995 respectively.

#### Analysis of diet

Stomach contents were analysed as described in Batchelor and Ross (1984) and Klages *et al.* (1992). After collection, each sample was weighed (to the nearest gramme) and sorted into individual prey components. Components were counted, measured and weighed. The number of prey items was determined from intact fish or squid and from the number of caudal fins of digested fish in each food bolus. The fork length ( $FL$ ,  $\pm 2$  mm) of measurable fish and the dorsal mantle length ( $DML$ ) of squid were recorded. Prey species were identified directly, when prey was sufficiently intact, or by examination of otoliths or squid beaks. Identifications of hard-part remains were confirmed by comparison with the reference collections of otoliths and squid beaks housed at the Port Elizabeth Museum. Sizes of partially digested prey were estimated from regressions, derived from the reference collections (Smale *et al.* 1995), which related dimensions of hard-prey remains to prey lengths and masses.

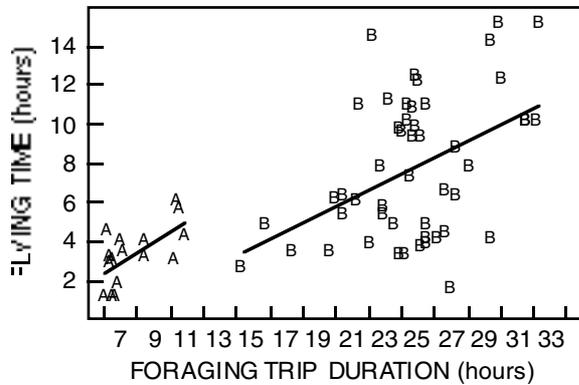


Fig. 2: Relationship between time flying and total foraging trip duration for Cape gannets attending chicks for (A) birds departing and returning within the day and (B) staying at sea overnight. The corresponding linear regression lines are also shown

### Activity recorder

The activity recorder was built from a digital wrist-watch, modified so that time-keeping stopped when external electrodes were shorted during water immersion (Cairns *et al.* 1987a). Recorders were secured to the leg of gannets, below the normal water line of the body when at the surface, using two plastic electrical cable-ties inserted through four brass eyes cast into the resin surrounding the watch. The technique allowed for quick attachment and removal of the timer. The time spent on or under the water was the difference between the total observation period and the time by which the foot-mounted watch advanced. Because time on land was known from direct observations, flight time of gannets could be calculated as the total time the watch had advanced, less the sum of time on land and time spent on or under water.

Although watch time was recorded to the nearest minute, the sampling regime resulted in the estimate of time active being accurate to the nearest 15 minutes only. Gannets are restricted to foraging in the upper 13 m of the water column (Adams and Walter 1993), with a mean dive time of four seconds (Duffy 1989). Consequently, it was considered that the time of swimming activity underwater was insignificant in relation to the total foraging trip duration, and that measurements of time flying correlated with distance travelled and, hence, foraging effort. Activity budget data were integrated with measurements of reconstituted meal mass and prey composition. Accordingly, prey choice could be examined in relation to foraging effort.

### Handling effects

In order to evaluate the effects of manhandling and attachment of timers on the behaviour of Cape gannets, patterns of arrival and departure of 30 adult birds attending chicks in a group of 15 minimally disturbed nests (controls) were examined. Direct disturbance to marking of the birds was limited by dabbing a picric-acid-soaked sponge on the end of a 2-m long pole. Partners at individual nests were identified by marking either on the chest or back. The presence or absence of individual birds was recorded at 15-minute intervals from dawn and dusk for seven consecutive days.

## RESULTS

### Foraging trip duration

Mean foraging trip durations (*FTDs*) of Cape gannets in the control group were  $15.7 \pm 8.8$  ( $n = 142$ ). However, they were bimodally distributed (Fig. 1), indicating that most birds either returned the same day that they left (mean =  $7.7 \pm 2.9$  h) or that they remained at sea overnight and returned the following day (mean =  $20.9 \pm 4.3$  h). A few birds stayed away for two consecutive nights. *FTDs* of metered birds were longer (mean =  $23.5 \pm 10.4$  h,  $n = 86$ ) than for the unmanipulated control group (see above). Mean *FTDs* of birds returning the same day they left and those returning after spending overnight at sea were  $7.8 \pm 1.8$  h ( $n = 16$ ) and  $27.3 \pm 7.9$  h ( $n = 70$ ) respectively.

The more frequently recorded short trips (<1 day) of minimally disturbed birds (44.9% of all trips) compared to those of metered birds (21.1% of all trips) suggests some behavioural consequences associated with handling of birds for attachment of meters. However, differences may partially reflect the bias inherent in the deployment procedure. A greater proportion of birds leaving early in the day returned the same day they departed, compared to birds leaving later in the day. Consequently, minimally disturbed birds departing before 09:00 had foraging trips (median = 8.3 h,  $n = 44$ ) significantly shorter (Mann-Whitney rank sum test,  $p < 0.0001$ ) than birds leaving after 09:00 (median = 18.3 h,  $n = 110$ ). Although deployment of activity meters took place between 06:24 and 16:44, 72% of attachments occurred after 09:00. However, even when comparison of *FTDs* between the control group and the metered group was restricted to birds departing before 09:00, there remained a significant difference (Mann-Whitney rank sum test,  $p < 0.0001$ ,  $df = 68$ ,

Table I: Composition of stomach contents of metered Cape gannets sampled on return to the colony after foraging, expressed as percentage by number, mass and frequency of occurrence (FO)

Prey	Number	% Number	Mass (g)	% Mass	FO	% FO
<i>Sardinops sagax</i>	266	40.0	21 816.3	61.1	54	69.2
<i>Engraulis capensis</i>	348	52.3	6 440.6	18.1	32	41.0
<i>Scomberesox saurus</i>	11	1.7	1 089.6	3.1	9	11.5
Other species	40	6.1	6 333.2	17.8	14	18.0

$n = 44$ ) indicating that this result was not merely an artefact of the timing of the deployment.

### Activity budgets

From 86 birds originally equipped with activity meters, data from 76 individuals were obtained, representing 2 023 h of monitoring. The rest of the meters malfunctioned or were lost. Seven birds behaved markedly different from all the others. According to the time shown on the foot-mounted watch, one bird never sat on the water and six others spent most of their time away from the nest flying (mean = 78.5%, range 74.5 – 84.2%).

The majority of the birds ( $n = 69$ ) behaved in a broadly similar manner. Metered Cape gannets returning within the same day to their nest spent  $41.8 \pm 16.2\%$  ( $n = 16$ ) of their time at sea and out of the water (flying and/or gliding), and the flying time was significantly correlated with the total duration of the foraging trip ( $r = 0.63$ ,  $p < 0.01$ ,  $n = 16$ , Fig. 2). Birds that stayed away overnight also showed a significant correlation between FTD and flying time ( $r = 0.48$ ,  $p < 0.01$ ,  $n = 53$ ), although the activity data suggest that resting time of gannets at night was variable (Fig. 2). As visual hunters, Cape gannets are effectively prevented from successful foraging during the night, defined here as the period between twilights. Darkness lasted approximately 7.5 h during the study period in midsummer. If FTDs are adjusted accordingly (i.e. shortened by this amount of time), the mean flying time of this group was  $45.3 \pm 18.8\%$  ( $n = 53$ ), similar to the percentage obtained for birds that only made day trips.

### Diet

In all, nine prey species were recovered from the stomachs of 78 metered birds. The majority of stomachs contained individuals of one species only. Diet was dominated by sardine and anchovy (Table I). The higher proportion of sardine compared to anchovy, when expressed as proportion by mass, reflects its larger average mass ( $82.1 \pm 22.2$  g v.  $20.0 \pm 8.7$  g respec-

tively). This is reflected also in the number of fish per regurgitation ( $3.5 \pm 1.8$  for gannets returning with sardine and  $7.4 \pm 5.4$  for gannets returning with anchovy). Regurgitation mass of gannets averaged  $220.2 \pm 121.4$  g ( $n = 78$ ), within the range recorded from samples in previous years (Klages *et al.* 1992).

### Food accumulation rate

The evaluation of food accumulation rate by gannets in relation to foraging effort is complicated by potential digestion during the course of a foraging trip. A bias of this nature is likely to increase with increasing foraging trip length. Consequently, data only from birds that did not remain away at sea overnight were considered, which restricted the analysis to the 11 gannets returning with sardine only. Five birds that spent less than one day at sea returned with other prey species.

Food intake of foraging Cape gannets, determined as the mass of reconstituted stomach contents or the total increase in mass of the adult gannet from departure to return, was not significantly correlated with foraging effort measured as total foraging trip duration ( $r = 0.52$ ,  $p > 0.05$ ) or flying time ( $r = 0.19$ ,  $p > 0.05$ ).

The difference in mass of gannets, over and above the mass of stomach contents, returning the same day ( $133.1 \pm 144.4$  g,  $n = 27$ ) and those that stayed at sea overnight ( $190.5 \pm 172.4$  g,  $n = 57$ ) was not significant (Mann-Whitney rank sum test,  $p > 0.05$ ).

### Prey choice and foraging effort

FTDs or the relative time spent flying as a proportion of the total foraging trip of gannets returning with sardine were not significantly different ( $p = > 0.05$ ) from birds returning with other prey (Table II). However, birds returning with sardine spent significantly less time flying than birds returning with other prey ( $p < 0.05$ , Fig. 3). Consistent with this, estimated energy consumption per foraging trip was lower and the ration of surplus energy consumption was higher for birds returning with sardine compared to those returning with other prey (Table III).

Table II: Foraging effort (time flying) over the course of a foraging trip for Cape gannets returning with sardine and other prey

Prey	Mean flying time in hours $\pm 1$ SD	Median flying time in hours (25 and 75 percentiles)
Sardine	6.4 $\pm$ 4.7	5.1 (3.5 and 8.3)
Other prey	8.8 $\pm$ 5.1	8.4 (4.4 and 12.3)
All prey	7.7 $\pm$ 5.0	6.1 (3.9 and 10.9)

## DISCUSSION

### Foraging trip duration and activity budgets

Most Cape gannets attending chicks had *FTDs* of less than 24 h, consistent with their coastal feeding areas (Berruti 1987) and the distribution of their main prey species over the continental shelf (Hampton 1992). This bimodal distribution of foraging trip durations indicates that foraging is a largely diurnal activity (Fig. 1). This suggests that unsatiated birds choose to remain at sea overnight, roosting on the surface and feeding the next day, rather than returning to the colony.

Bimodal frequency distributions of foraging trips have been previously noted for some seabirds (Weimerskirch *et al.* 1994). Those authors considered that short trips allowed adults to increase feeding frequency to chicks, albeit at a cost to the adult's body condition, and that long foraging trips were recovery trips. The lack of a significant difference between mass increase of gannets recovered after foraging trips conducted within a

Table III: Estimated energy consumption and ratio of surplus energy to energy consumption of Cape gannets returning with sardine and other prey. Values are estimated over individual foraging trips for adult birds attending chicks. Estimated energy consumption was calculated from flight costs (Birt-Friesen *et al.* 1989) and assuming resting at sea was equivalent to incubation or brooding costs (Adams *et al.* 1991). Surplus energy accumulated over a foraging trip was calculated as the energy equivalent of mass of the regurgitated food sample plus any additional mass gain. Metabolizable energy values of sardine and anchovy were taken from Cooper (1978) and Batchelor and Ross (1984)

Prey	Mean energy consumption in kJ $\pm$ SD	Median ratio of surplus energy to energy consumption (25 and 75 percentiles)
Sardine	5 827 $\pm$ 1 119	0.37 (0.27 and 0.47)
Other prey	6 488 $\pm$ 1 273	0.30 (0.21 and 0.47)

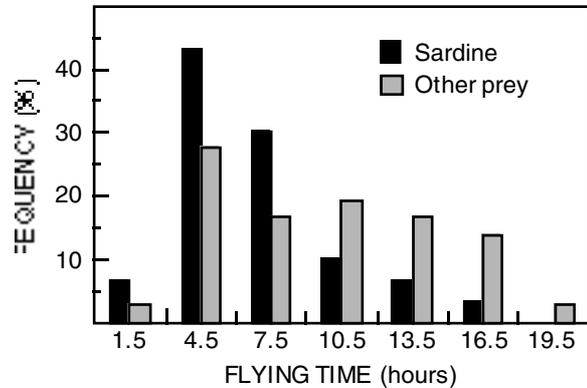


Fig. 3: Relative frequency of occurrence of the time spent flying during a foraging trip in relation to the prey species captured by foraging Cape gannets

day and those for birds at sea overnight suggests that this strategy was not adopted by Cape gannets.

The relatively short time spent flying (c. 40%) may provide adult gannets with the flexibility to buffer short-term variations in prey availability when feeding chicks. Burger and Piatt (1990) speculated that time budgets are most flexible in seabirds that lay only a single-egg clutch, such as gannets, as this precludes brood size adjustments. Given that provision of food by seabirds rearing chicks may be regulated by chick demand rather than food availability (Pugesek 1981, Shea and Ricklefs 1985, but see also Ricklefs 1987), flexible time budgets have important implications for the use of seabird data to assess prey availability. Biological parameters such as chick growth rates, which purport to reflect food availability, in fact may show poor correspondence if birds are able to respond to decreased food availability by increasing foraging time (Cairns *et al.* 1987b). Therefore, measurements of foraging effort with food intake rates corrected for digestion and maintenance costs of foraging adults are more likely to provide indices useful for direct monitoring of prey abundances.

The apparently adverse response of gannets to the manhandling associated with the attachment of meters has been demonstrated previously for Cape gannets (NJA, unpublished data) and for Northern gannets *Morus bassanus* (Birt-Friesen *et al.* 1989). The activity meters used here were small (<0.5% body mass) and were mounted at the back of the leg. In this position, they remained pressed against the body during flight. Consequently, it is suggested that the meters have a negligible effect on the ability of gannets to catch prey, but that their longer absence from the colony reflects

a behavioural response to manhandling rather than inefficient prey capture. This disturbance effect does suggest some caution in interpretation of the present activity budget. However, most of the analyses are based on measurements of flying time as an estimate of foraging effort and therefore are unlikely to be affected by disturbance effects.

### Food intake and prey distribution

The relationship between food intake and foraging effort may provide inferential evidence of prey distribution encountered by seabirds (see Wilson 1985). For predators feeding on small, randomly distributed shoals that are rapidly depleted, a positive correlation would be expected between foraging effort and food intake (Wilson 1985). Birds must encounter numerous small patches of prey before accumulating sufficient food, and the farther a predator travels the more food it is likely to encounter. Such correlations have been demonstrated for both African penguins (Wilson 1985) and Adélie penguins *Pygoscelis adeliae* (Chapell *et al.* 1993). However, for Adélie penguins, it was also shown that foraging trip duration was related directly to distance from the colony or the nearest pack ice (Ainley *et al.* 1998). The present results do not demonstrate any such positive correlation between food intake, measured as stomach content mass and bird mass increase at the conclusion of a foraging trip, and foraging effort of Cape gannets returning with sardine. This suggests that gannets were feeding on large, spatially unpredictable fish shoals that provide a substantial part of the stomach capacity of gannets at a single encounter. Also, the availability of such shoals was relatively high, i.e. not limited.

### Prey choice and foraging effort

The present hypothesis that sardine is the most profitable prey species for Cape gannets assumes that gannets forage optimally. This assumption has yet to be demonstrated. Despite criticisms of this approach, particularly in regard to the behaviour being optimized (see Stephens and Krebs 1986), a number of aspects of the biology of Cape gannets suggest that the present approach is valid. Predation rates at sea are low and much of the social interaction between gannets associated with breeding occurs at the colony (Nelson 1978). Consequently, foraging by gannets is likely to be conducted independent of most other activities. Given that flying by gannets is energetically expensive (Birt-Friesen *et al.* 1989, Adams *et al.* 1991), they are likely to maximize net energy gain over the course of a foraging trip by minimizing their time flying. Finally, the suitability of a particular prey species to gannets

is likely to reflect its size and energy content rather than the composition of other nutrients which are presumed to be similar for many pelagic fish prey (Ricklefs and White 1981).

Models of prey choice by optimal foragers (Stephens and Krebs 1986, Kamil *et al.* 1987) predict, first, that when the more profitable prey is very abundant, the predator should specialize on it, second, that the availability of the less profitable prey should have no effect on the decision to specialize on the better prey, and third that, as the availability of the most profitable prey increases, there should be a change from no preference (the predator eats all prey types) to complete preference. The marine environment is dynamic, with conditions varying between foraging trips. Accordingly, foraging gannets have incomplete knowledge of their environment. This fact, coupled with variance in the value of the threshold encounter rate of preferred and alternative prey at which switches in diet are predicted, will result in deviation from zero-one rule. Consequently, partial preferences are expected. In common with many other studies (see Stephens and Krebs 1986), the gannets under study did not show the all-or-nothing preference rule.

The present results show that foraging effort, measured as flying time, was less for breeding Cape gannets returning with sardine than for birds returning with other prey species. Consistent with this, estimated energy consumption per foraging trip was lower and the ratio of surplus energy to energy consumption was higher for birds returning with sardine compared to those returning with other prey (Table III). These findings support the conclusions of Batchelor and Ross (1984) and Berruti and Colclough (1987), based solely on the physical characteristics of the prey, that sardine are the preferred prey of gannets.

Consequently, the proportion of sardine in gannet diet is indeed predictive of its abundance at appropriate spatial scales, at least at low-to-medium sardine biomass (see Berruti and Colclough 1987, Montevecchi and Berruti 1991). A further consequence of this demonstrated preference is that fluctuations in the availability of sardine could produce large shifts in the relative harvests of other prey by gannets, but not necessarily vice versa.

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